

ECOLOGICAL MONOGRAPHS

VOL. 10

APRIL, 1940

No. 2

BERKSHIRE PLATEAU VEGETATION, MASSACHUSETTS¹

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¹ Contribution from Osborn Botanical Laboratory, Yale University. Received for publication, February 10, 1939. The material here presented is included in a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Yale University. The work was supported in part by an Eaton Scholarship and a University Fellowship in the Graduate School of Yale University during the academic years 1934-35 and 1935-36.

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BERKSHIRE PLATEAU VEGETATION, MASSACHUSETTS

INTRODUCTION

NATURE OF THE PROBLEM

The present paper embodies certain results of botanical investigations in the Berkshire plateau of western Massachusetts, a well-defined physiographic province characterized by forests of red spruce (*Picea rubra*), balsam fir (*Abies balsamea*), hemlock (*Tsuga canadensis*), white pine (*Pinus strobus*), beech (*Fagus grandifolia*), yellow birch (*Betula lutea*), sugar maple (*Acer saccharum*), and oaks (*Quercus* spp.). The problem undertaken was two-fold: first, to make an extensive and primarily empirical field reconnaissance of the vegetation, supplemented by local intensive studies; and second, to organize the material thus obtained in accordance with those ecological concepts most practicable for the presentation of the data.

METHODS OF INVESTIGATION

The factual basis for the present paper has been derived mainly from field studies conducted over a period of twenty-five weeks during the summers of 1934 and 1935. At all times, emphasis was on extensive rather than on locally intensive investigation. Approximately three hundred stations were temporarily established, at each of which were recorded floristic lists, autecologic data, and notes on vegetation structure based upon quadrat studies and general observation. This information was supplemented by survey notes taken at frequent intervals on practically the entire road mileage of the Plateau, on all important trails, and on many cross-country trips in sections not otherwise covered.

CONCEPTS AND NOMENCLATURE

Although many workers have attempted to correlate the concepts of investigators in ecology and to standardize the terminology, these essays generally have not been successful. In all comparisons, in botanical as well as in other sciences, three distinct aspects of the problem must be recognized: (1) the nomenclature used; (2) the concretion, or the actual facts perceived and studied; and (3) the abstraction, or generalization from the facts. The last is an extension of the concrete concept, including material with which the investigator may not be personally acquainted. The use of an established system of concepts and nomenclature can be in reference to one or more of these three aspects, independently of the others. The limitation is always recognized in this paper.

It has been found necessary to differentiate, as have Tansley and Chipp (1926), between two concepts which can best be identified by the terms "flora" and "vegetation." The former is used to refer collectively to all kinds

of plants of a region, each kind being of equal importance as a floral element. The term vegetation is used to refer to the actual plant cover, in which case interest is centered upon its nature and character in respect to structure, growth form, physiognomy, dominance and distribution of certain species, and the effect of ecological factors. Accepting this distinction, adjacent areas may have essentially the same floras but distinctly different vegetation types, as, for example, the Illinois prairies and the Indiana forests. Conversely, proximate sections of the country may have different floras but essentially the same type of vegetation, as the plains and the prairies.

The term "community," following Tansley and Chipp (1926), is used to embrace any grouping of plants worthy of study as a vegetation unit because of reactions of the species among themselves and with the environmental factors. More than one community may exist on the same site at the same time or at different times. Layer communities are examples of the first condition; seasonally determined communities are examples of the second. The term community is not restricted to include the entire plant population of a site.

The word "evolution," as used in French literature, is preferred to "plant succession" when reference is made to gradual change or development of the vegetation in time, rather than to conditions of abrupt transformation from one community to another.

"Predominant," as used by animal ecologists, refers to an apparent abundance or numerical frequency of an organism, without any implication as to the role of the species in the dynamics of the community. It is so used in this paper.

Nouns, as plateau and area, are capitalized in the text when they refer specifically to the Berkshire plateau, or to any or all of three areas to be defined below. Words such as frequency, abundance, and constancy, are capitalized only when used as phytosociological concepts.

When the author of a scientific name is not given, the nomenclature is that of Gray's *New Manual of Botany* (Robinson and Fernald, 1908).

PREVIOUS INVESTIGATIONS

The high commercial value of the coniferous and of the mixed deciduous and evergreen forests of northern New England has greatly stimulated their investigation with particular regard to silvicultural problems. In central and southern New England, though forests are less extensively distributed, research has been favored by the establishment of several experimental areas under the jurisdiction of forestry schools of the vicinity. Ecological conditions on the Berkshire plateau, however, and the characteristics of its vegetation have been known only in a general manner.

Three ecologists have been directly concerned with the area in question. Nichols, in his studies of Connecticut vegetation (1913a, 1913b, 1914, 1915, 1916) includes a description of the relatively northern type of forest growth

formerly existing in the towns of Norfolk and Colebrook, a region included in this study. His account (1913b) of the virgin forest at Colebrook is a necessary adjunct to the present paper, as no such stands now exist. Lutz's investigation (1928) of upland forest successions of southern New England also concerns the forests of Colebrook and vicinity, but the distinct boreal character of this locality is implied rather than stated. Stafford (1931) has discussed a system of forest planting in the Swann State Forest in Monterey, Massachusetts, and a brief outline is given of old field successions in the immediate vicinity. A survey by counties of the cover types of Massachusetts has been made by Cook (1929); this paper does not directly afford any data concerning the forests of the Plateau. The flora of Berkshire County has been the subject of an investigation by Hoffman (1922), and this has been referred to frequently in the preparation of the manuscript of the present paper.

ACKNOWLEDGMENTS

I should like to acknowledge my indebtedness to Dr. G. E. Nichols, Yale University, for his continual and careful supervision of this study, and to Dr. W. S. Cooper, University of Minnesota, under whom the problem was initiated and from whom assistance has been continually received. I also wish to express appreciation for courtesies extended during the course of the study by: W. Arnold, Institute of Geographical Exploration, Harvard University; J. F. Dubuar, New York State Ranger School; J. J. Fritz, Middlebury College; G. G. Goodwin, American Museum of Natural History; R. C. Hawley, Yale University; H. J. Lutz, Yale University. L. E. Partelow has prepared Figs. 2 and 5; H. F. A. Meier, R. R. Hirt, and J. L. Lowe, New York State College of Forestry, have made valuable comments on the manuscript.

PHYSIOGRAPHIC FEATURES

The local geological features of southern New England, with more or less particular reference to western Massachusetts, are well summarized in the works of Emerson (1917), Knopf (1927), Flint (1930, 1934), Lobeck (1922), Prindle and Knopf (1932), and Fenneman (1938), whose publications are used as a basis for the following paragraphs.

The New England geological province is represented in western Massachusetts by several sections, all extending from north to south across the state. One of these is the Berkshire plateau (Fenneman), 25-30 miles in width, extending 55 miles from Vermont on the north to Connecticut on the south. This plateau is flanked on the east by the Connecticut Lowland (Lobeck), a peneplain on weak Triassic sandstones, with an elevation of about 300 feet above sea level; it is bounded on the west by the Berkshire Lowland (Lobeck), a peneplain underlain by early Paleozoic limestones, of about 1,000 feet elevation.

The rocks of the Plateau are pre-Cambrian and early Paleozoic, with some formations of Devonian and Carboniferous age. The strata are highly metamorphosed schists and gneisses of sedimentary and igneous origin, complex in structure and difficult of interpretation. The varying nature of the underlying rocks within the Plateau does not appear to be significant in determining or affecting the general types of vegetation now in existence.

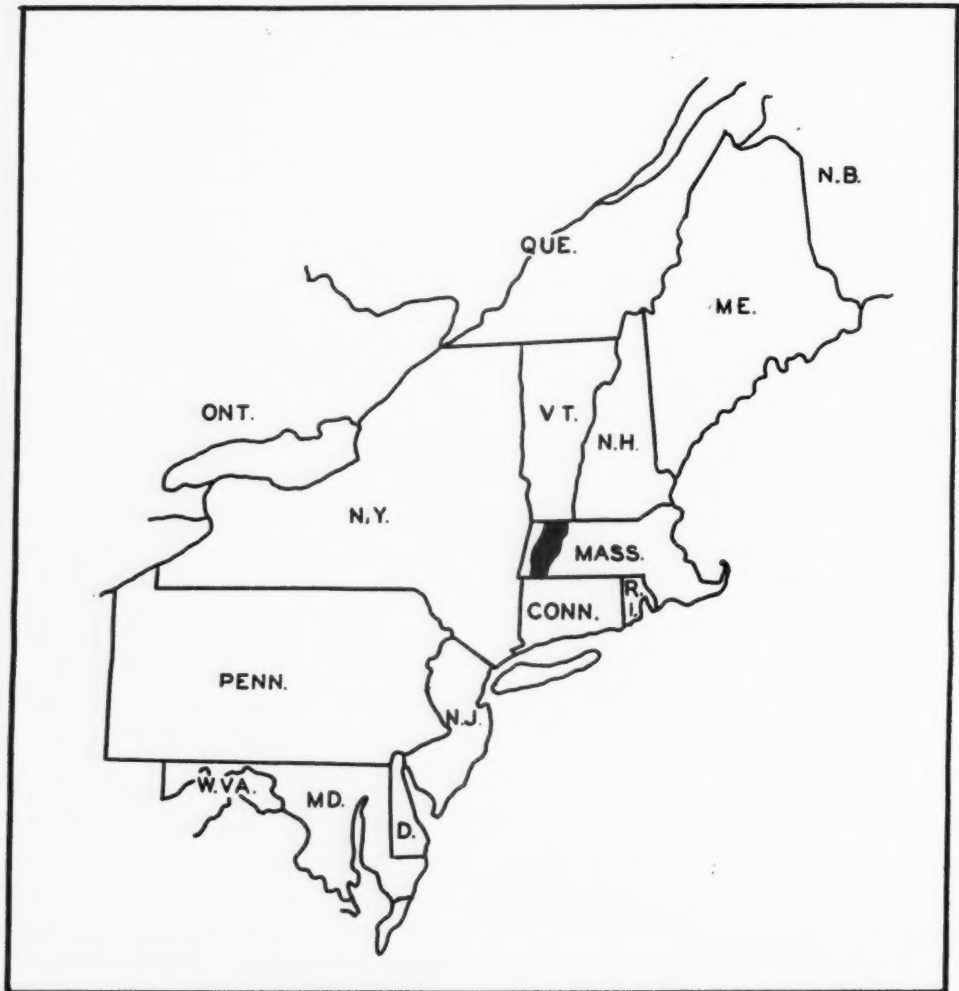


FIG. 1. Map of east-central North America, showing the location of the Berkshire Plateau in Massachusetts.

In respect to topography, the Plateau is an uplifted complex of erosion levels standing at about 2,000 feet in the northwest, 1,500 feet in the southwest, and with accordant summits above 1,000 feet along the eastern margin. The descent to the adjacent lowlands is gentle on the eastern front; it is abrupt on the western side where, in the north, the impressive escarpment is known as the Hoosac Range. The average relative relief on the Plateau is 200 to 300 feet. The region is characterized by a continuous succession of

hills and V-shaped valleys, indicating a pre-glacial condition approaching maturity in the erosion cycle. Interior lowlands, poorly drained sites, flood plains, escarpments, cliffs, tali, rocky domes, and monadnocks are relatively rare. The "general upland" type of topography predominates areally, and provides a relatively uniform physiographic habitat for vegetation.

The action of Pleistocene glaciation on the preexisting topography resulted in a smoothing of the contours and a reduction of the relative relief. Glacial erosion apparently was restricted to a removal of the mantle and scouring of the rocks at the higher elevations; widening and deepening of valleys is not conspicuous. Upon stagnation of the ice sheet a stony till 10 to 50 feet in thickness was deposited indiscriminately on almost all surfaces. Along the major stream valleys gravelly and sandy terraces developed; these have now been appropriated largely for agricultural purposes. On the Plateau, the various types of upland glacial topography do not appear to be correlated with the major types of vegetation.

CLIMATIC FEATURES

Climatic conditions of the Berkshire plateau are more boreal than those of the adjacent lowlands, although in general features they resemble those of the Connecticut and Berkshire valleys. Hydrotherm figures (according to Raunkiaer, 1907) are given for Williamstown, Pittsfield, and Springfield (Fig. 2).

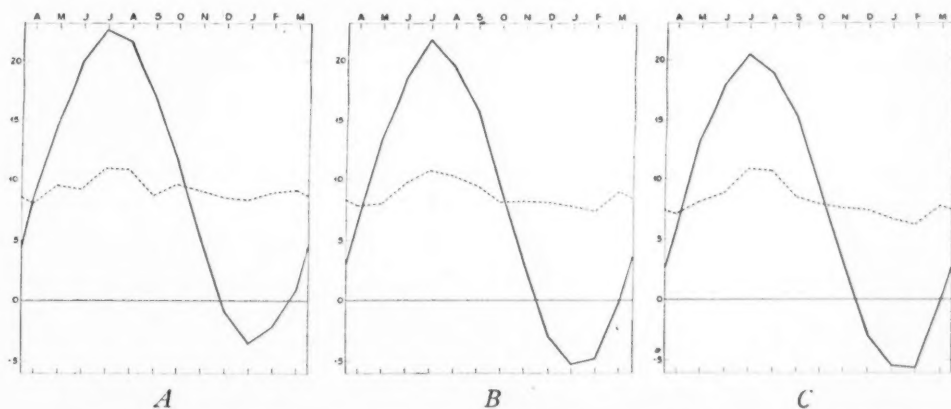


FIG. 2. Hydrotherm figures for Springfield (A), Pittsfield (B), and Williamstown (C), respectively. Numbers on the vertical lines denote both degrees Centigrade and centimeters of precipitation. Letters on the horizontal lines denote the months of the year. The solid line is the temperature curve; the broken line is the precipitation curve.

The average annual precipitation varies from 38 to 46 inches in western Massachusetts and from 42 to 45 inches on the Plateau. The seasonal distribution of rainfall is relatively uniform, with December, January, and February as the driest months. Snow usually covers the ground throughout the winter season, although the spring advances with sufficient slowness so that

floods of destructive magnitude are of infrequent occurrence. Periodic droughts do not occur, nor do cloudbursts. Fogs in summer are occasional at the higher altitudes.

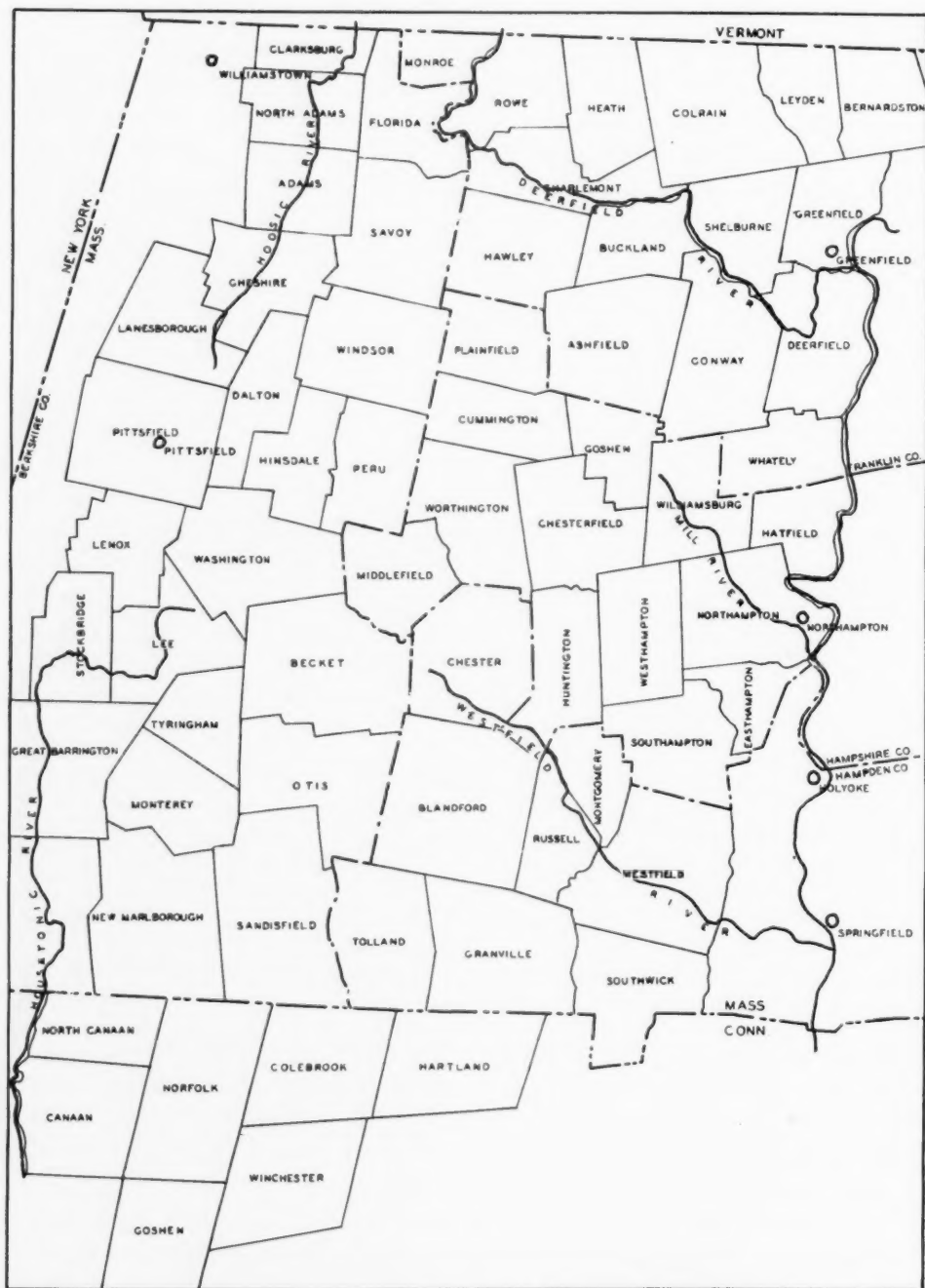


FIG. 3. Map of western Massachusetts, showing the larger rivers, the counties, townships, and the more important cities.

In temperature conditions, the high Plateau is cooler than the surrounding lowlands. According to the map compiled by P. Church (in Wright, 1933), the upland has a growing season averaging 120 to 130 days, with extremes probably varying from 90 to 170 days, whereas the Connecticut Lowland has a season averaging 170 days. These conditions can be correlated with the upland vegetation types only in a general way. To the contrary, from personal observations in the Town of Norfolk, Connecticut, the interval between killing frosts was found to be six weeks to two months longer on an upland ridge than in a valley bottom 2 miles away, a condition which is in agreement with similar observations of Wright (1933). It has been found that for minor variations in topography, killing frost intervals and plant growing seasons are correlated indirectly. This is apparent in the valley bottoms by the more rapid development of spring vegetation and by the frequent presence of southern species not found on the slopes above.

Both Köppen (1923) and Thornthwaite (1931) include the plateau in a climatic region which embraces the Great Lakes area and the St. Lawrence Valley. Köppen characterizes the region in its entirety as boreal, constantly moist at all seasons, with cold wet winters, with the temperature of the warmest month less than 22°C ., and with the temperature of more than four months greater than 10°C . Thornthwaite characterizes it as humid, with adequate moisture at all seasons, and with a low temperature efficiency of a summer concentration of 50 to 69 percent.

EDAPHIC FEATURES

County soil survey bulletins have been published by the United States Department of Agriculture for Berkshire, Franklin, Hampshire, and Hampden counties, thus covering all of western Massachusetts, and from these bulletins the following generalizations are drawn:

The soils of western Massachusetts may be classed into four groups on the basis of the nature of the parent material: (1) glacial till, (2) old water-laid terrace materials, (3) recent alluvium, and (4) miscellaneous materials such as rough stony land (immature soils, with profile undeveloped), muck, and meadow. On the Plateau, the old terraces although agriculturally important are limited to the narrow valleys. Mucks and poorly drained soils occupy scarcely 1 percent of the total area, and recent alluvium occurs rarely if at all. Thus, immature soils of stony lands and soils derived from glacial till cover almost all of the Plateau. This glacial till consists largely of materials similar in their lithologic characteristics to the underlying rock and, as weathering seldom has altered the soil to depths greater than 1.5 to 2.5 feet, the character of the parent material is always important in the recognition of the soil types.

At altitudes above 1,200 to 1,300 feet on the Plateau (in regions to be designated later as the Blandford and Savoy areas), the soils show in the A horizon a definite eluviated layer which may attain a thickness of 2 inches.

In some virgin soils where this is absent, a brown or coffee-colored layer exists. This soil relates the area with the podzol region lying to the north, while distinguishing it from the low hills along the eastern margin (later to be segregated as the Deerfield River Area) which are part of the region of "gray-brown podzolic soils" (Marbut, 1935, and Kellogg, 1936) of east-central United States.

A representative podzol profile on the uplands consists of the following layers: (1) a thin layer of litter, (2) a layer of dark brown leaf mold 1 to 1.5 inches thick, (3) a thin layer of finely divided organic matter, the raw humus, (4) a podzolized layer of light gray soil, from 0.5 to 2 inches thick, often thinner, or entirely absent, (5) a 1-inch layer of deep brown soil, mellow and fluffy, and never indurated, (6) a layer 12 to 18 inches thick, of yellowish-brown slightly heavier material, which grades into yellow, less weathered parent material, and (7) gray unweathered or only slightly weathered parent material.

Whereas the soils of the Connecticut Lowland are rather heterogeneous, ranging from silt loams to sands, those of the Plateau are uniformly loams and sandy loams, usually heavier in texture and with compact substrata. They are distinctly acidic in reaction, the pH of the A and B horizons usually ranging from 4.0 to 5.5. Limestone influences are absent, except in the northeastern part of the Plateau, where beds of impure limestone alternate locally with the schist. In conclusion it may be said that strong contrasts in edaphic conditions within the area of the podzol soils do not exist, and that the more important differences in upland vegetation which do occur, bear no apparent correlation with soil differences.

ANTHROPIC¹ FEATURES

Details of the pre-colonial history of western Massachusetts have not been obtained other than statements that the Indian population was very small. In all probability the Plateau, except for the foothills of the east and south, never suffered from the repeated fires which were used by the Indians to destroy the scrubby growth and which have played an important part, according to Bromley (1935), in the history of the vegetation of the rest of southern New England.

The rugged Plateau, because of its relatively unfavorable climate, was one of the last sections of Massachusetts to receive settlers. The majority of the farms here were first developed during the latter part of the eighteenth century, although the region was never completely occupied. After the first half of the nineteenth century, when the wealth including that accruing from the sale of timber had been dissipated in clearing and tilling a stony soil, a satisfactory standard of living could not be maintained. Within a few gen-

¹ The form "anthropic" is used, following Domin (1929). This word is derived from *ανθρωπικος*, which is the adjectival form used in the derivation of such words as edaphic, geographic, biotic, and genetic. Nichols (1923) has proposed "anthropeic," derived from *ανθρωπειος*; and this form has been adopted by Lutz (1928 and 1934). Gleason (1927:306) has used "anthropoic."

erations, an exodus of the farming class began that is continuing to the present time. This depopulation and abandonment of farms is in marked contrast to the many cities and the flourishing agriculture in the Connecticut and Berkshire Lowlands. Aside from the towns in the low-lying valleys of the Deerfield and Westfield rivers, there are no villages with a population of more than a few hundred on the highlands of the Plateau. Associated with the abandonment of farm lands has been a progressive decrease in the intensity of grazing of farm lots and their eventual abandonment and reversion to forest. Since at least 50 percent of the land has been pastured at one time or another, the existing vegetation of the Plateau is conditioned largely by this phase of its history.

Today the forested areas occupy the steeper slopes and the rockier soils. In the northern and higher parts of the Plateau, forests have been less affected by man than in the more settled areas, where they have been heavily exploited for cordwood and occasionally stripped for charcoal. In almost all cases, cutting of timber has been on short rotation and mature and overmature stands are rare. Usually clear-cutting is practiced, although occasionally all timber is removed except hemlock. Such selective cutting does not alter the composition of the forest in respect to hemlock. On the other hand, in many northern townships selective cutting of spruce has so completely removed this tree from the upper canopy that the aspect of large areas of forest has been considerably altered. Apparently no original pre-colonial forests remain on the entire Berkshire plateau.

Fire and grazing are two destructive factors significant in most disturbed areas. Fire as an active ecological factor on the Plateau, however, is almost non-existent. Less than one percent of the forest land has suffered from recent severe burns, and pyric cover types comparable with the aspen stands of the Adirondacks cannot be distinguished. Furthermore the practice of annual burning of fields and woodlands is unimportant. Intensive grazing of forests, so destructive to timber in many parts of the Middle West, has not occurred on the Plateau, although grazing has induced large acreages of distinctive pasture vegetation on clear-cut lands.

Within the past decade, important changes in ownership of land have occurred that may vitally affect the economic position of the Plateau as well as alter its aspect and its general vegetation. Large tracts have been purchased for natural watersheds and reservoir sites, while other and larger units are being acquired for state forests. Parts of these are being intensively developed for recreational use; the forests of other sections are being selectively thinned and culled. Reforestation of old pasture lands by planting of evergreen conifers is progressing rapidly. All these activities are changing the composition of the forests to a great extent, as well as totally destroying much of the shrubby and herbaceous strata. No move has been made as yet by the State to give adequate protection to certain scenic roadside features, especially the fields and pastures and the occasional overmature stands, all of which possess high recreational and scientific value.

Although chestnut (*Castanea dentata*) was never as important on the Plateau as in some adjacent regions, nevertheless it was a distinct component of the forest at the lower elevations. The complete destruction of all mature individuals of this species by the chestnut blight has left only stump sprouts. The disease is thus causing a reorganization in the structure of the forest that must be interpreted in conjunction with the complexities due more directly to the activities of man.

FLORISTIC FEATURES

INTRA-PLATEAU CONDITIONS

During the course of the field work, considerable attention was directed to the geographical distribution within the area of certain vegetationally significant species. The facts obtained, presented in Table 1, show that there is a prominent austral element on the eastern and southern margins of the Plateau, particularly in the lower basins of the Deerfield and Westfield rivers. This is part of a flora well developed in southern New England and southward, which extends northward in three lowland areas, (1) the Hudson River Valley, (2) the Berkshire Lowland, and (3) the Connecticut Lowland. The Connecticut valley is distinctly more southern than the Berkshire valley in its floristic aspects; it is likewise a more pronounced topographic lowland, both in area and altitude. Edaphic conditions in some cases may be contributory factors in the distribution of this flora, as the generally high acidity of the plateau soils very likely militates against the spread and development of some of the southern species.

TABLE 1. List of trees, shrubs, vines, and common herbaceous plants more or less generally distributed in the lowlands and at lower elevations on the Plateau and, with certain exceptions, restricted in their occurrence to that part of the Plateau to be designated the Deerfield River Area.

<i>Juniperus virginiana</i>	<i>Quercus montana</i> , Willd. ⁴
<i>Pinus rigida</i> ¹	<i>Quercus muhlenbergii</i> ¹
<i>Populus deltoides</i>	<i>Quercus prinoides</i>
<i>Juglans cinerea</i> ¹	<i>Quercus velutina</i>
<i>Carya cordiformis</i> ⁴	<i>Celtis occidentalis</i>
<i>Carya glabra</i>	<i>Liriodendron tulipifera</i> ⁴
<i>Carya ovata</i> ⁴	<i>Sassafras variifolium</i> ⁴
<i>Quercus alba</i> ⁴	<i>Platanus occidentalis</i>
<i>Quercus bicolor</i>	<i>Acer negundo</i>
<i>Quercus coccinea</i>	<i>Acer saccharinum</i>
<i>Quercus ilicifolia</i>	<i>Nyssa sylvatica</i>
<i>Quercus macrocarpa</i> ²	
<i>Myrica caroliniensis</i> ³	<i>Celastrus scandens</i>
<i>Myrica asplenifolia</i>	<i>Staphylea trifolia</i>
<i>Alnus rugosa</i>	<i>Ceanothus americanus</i>
<i>Corylus americana</i>	<i>Vitis aestivalis</i>
<i>Berberis vulgaris</i> (introd.)	<i>Vitis bicolor</i>
<i>Benzoin aestivalis</i>	<i>Dirca palustris</i>
<i>Pyrus arbutifolia</i> var. <i>atropurpurea</i>	<i>Cornus circinata</i>
<i>Rosa carolina</i>	<i>Cornus florida</i>
<i>Xanthoxylum americanum</i>	<i>Cornus paniculata</i>
<i>Rhus copallina</i>	<i>Cornus amomum</i>
<i>Rhus glabra</i>	<i>Clethra alnifolia</i>
<i>Rhus vernix</i>	<i>Cephalanthus occidentalis</i>

Asplenium platyneuron
Asplenium trichomanes
Camptosorus rhizophyllus
Onoclea struthiopteris
Phegopteris hexagonoptera
Selaginella apus
Andropogon furcatus
Andropogon scoparius
Cenchrus carolinianus
Elymus canadensis
Arisaema dracontium
Orontium aquaticum
Symplocarpus foetidus
Tradescantia virginiana
Allium canadense
Allium tricoccum
Chamaelirium luteum
Polygonatum commutatum
Smilacina stellata

Smilax rotundifolia
Trillium cernuum
Uzularia grandiflora
Uzularia perfoliata
Hypoxis hirsuta
Comandra umbellata
Claytonia virginiana
Anemone cylindrica
Anemone quinquefolia
Anemonella thalictroides
Hepatica acutiloba
Menispermum canadense
Podophyllum peltatum
Sanguinaria canadensis
Dicentra cucullaria
Dicentra canadensis
Dentaria diphylla
Baptisia tinctoria
Geranium maculatum
Chimaphila maculata

¹ *Juglans cinerea* is found occasionally at intermediate elevations on the Plateau where, however, it is of poor development and low vitality.

² *Quercus macrocarpa* and *Q. muhlenbergii* are confined in western Massachusetts to the Berkshire valley.

³ *Myrica caroliniensis* is coastal in its general range, but on the eastern foothills of the Plateau it is locally common in upland pastures.

⁴ Detailed range maps for these species are on file with the Graduate School at Yale University. Each map shows the location of all stations on the Plateau where individuals were observed.

EXTRA-PLATEAU RELATIONSHIPS

The flora of the Berkshire Plateau is dominated by elements from two floristic centers in North America, the first lying in the region of the Great Lakes and the St. Lawrence Valley, the second in the southern Appalachians. These were recognized by Transeau (1905), whose "northern conifer forest center" and "deciduous forest center" were illustrated in terms of arborescent floral elements, although the nomenclature implies a possible confusion with vegetation types. They are based upon an empirical analysis of ranges of representative trees, shrubs, and herbs. Both may be correlated with existing climatic conditions which, as expressed by Transeau, are at an optimum at the center for the species concerned and become progressively more unfavorable in proceeding from that center. Despite the nomenclature, the flora of each is by no means restricted to one life form or growth form. Evergreen needle-leaved and winter-deciduous broad-leaved trees are found in each. Consequently the centers are not to be identified with the "northern conifer forests" and the "eastern deciduous forests" of general recognition. In general, southern floristic elements predominate in the pitch pine, scrub pine, oak, hickory, beech, and maple forests of east central United States. Elements of the northern floristic center predominate in the spruce-fir forests, the hemlock and northern hardwood forests, and the Lake States pine forests. All of these northern forests are characterized by plants of the Taiga, and for this reason the flora is here referred to as the "Taiga flora" of north-eastern North America.

The two centers recognized above are floristic units in rapport with contemporary conditions. They are not necessarily to be correlated with "centers

of distribution" of other authors in regard to origin of species, direction of migration, greatest numerical development of closely related species, abundance of individuals, dominance of species, greatest areal development of vegetation types, or unity of life form.

VEGETATIONAL FEATURES

Bray (1930), in his study of the vegetation of New York, established six vegetation zones, the distribution of which he had determined for the entire state. Bray's zones are concretions, not abstractions. They were mapped and described on a basis of thorough field study; they were not located and defined by *a priori* definition, nor was any suggestion made for their usage and application outside of New York. After personal interpretation and field observation, the author can state that each zone is characterized broadly by a homogeneous climate and flora; intrazonal variations of forest, scrub, and pasture are correlated with local differences in edaphic, anthropic, pyric, and historic influences. As a taxonomic system the zone is of unquestioned value in purely scientific investigations as well as in practical agriculture and forestry, and deserves far greater recognition than it has thus far received. It is noteworthy in that it places minor emphasis on conspicuous but often superficial differences between existing cover types, and stresses not only the major controlling floristic and climatic factors but also the potentialities of the sites for bearing cover types other than those now in existence.

Bray's zones of New York have been found to exist in essentially the same pattern in western New England. Three of these zones occur in the Berkshire Plateau: (1) Zone B, of "chestnut, oaks, hickories, tulip poplar, etc."; (2) Zone C, of "sugar maple, beech, yellow birch, hemlock, white pine, etc."; and (3) Zone D, with "dominant trees of Zone C, plus red spruce, balsam fir, and paper birch." These three regions on the Plateau, insofar as they are local examples of more widespread vegetation zones, are worthy of specific recognition, and are here designated as the Deerfield River area (Zone B), the Blandford area (Zone C), and the Savoy area (Zone D), only the last two of which are under special consideration in this paper (Fig. 4). The recognition and delimitation of these three permit two generalizations of scientific and practical value. In the first place, the flora, at least in regard to the vegetationally important species, is essentially uniform throughout each Area, and any one may therefore be correlated with a "floristic region," a unit of the related science of floristic plant geography. Furthermore, it may be assumed that the major environmental factors are sufficiently uniform in each Area so that each species—other things being equal—behaves similarly throughout in regard to growth, vigor, aggressiveness, and reproduction. Consequently ecological studies made at any place on the Plateau are applicable to other parts of the same Area, but not to other Areas even when these are situated in the immediate vicinity.

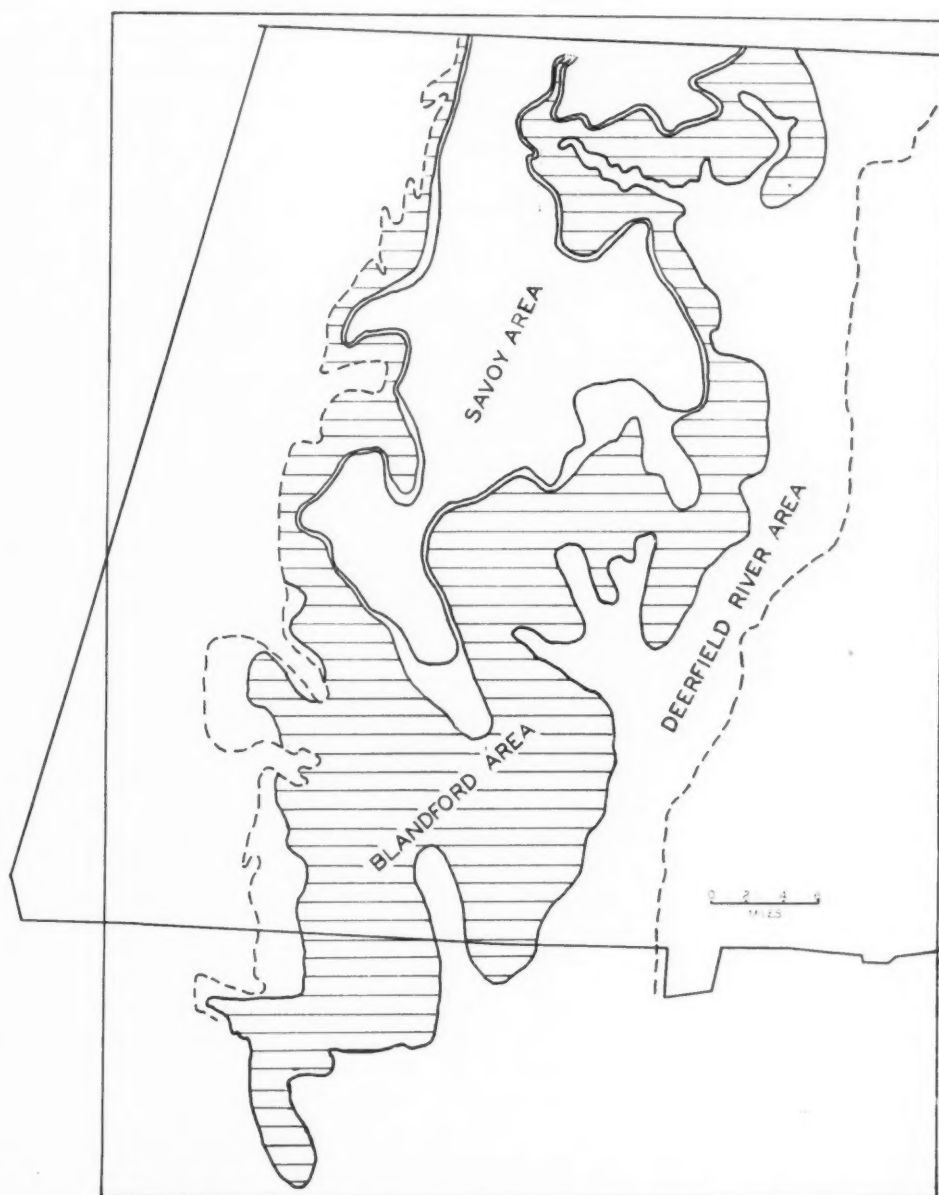


FIG. 4. Map of western Massachusetts, showing the location of the Deerfield River, the Blandford, and the Savoy areas, zones B, C, and D, respectively, on the Berkshire plateau.

The "general upland" type of topography is both areally predominant on the Plateau, and remarkably uniform in its ecological characteristics; extreme edaphic and topographic habitats, as flood plains and tali, are rare. Therefore, it is to the vegetation of the general uplands, to those lands which bear the bulk of the seminatural vegetation of today, that further discussion will be restricted. For purposes of analysis of this upland vegetation, certain specific communities have been established on a *posteriori* grounds. These are all of comparable value as vegetation units and are recognized because of

their general distribution and frequent occurrence. They are, moreover, specific for and limited in distribution to an Area, and the names applied are to be used in this limited sense only, or until future study in adjacent regions shows other communities to be identical with them.

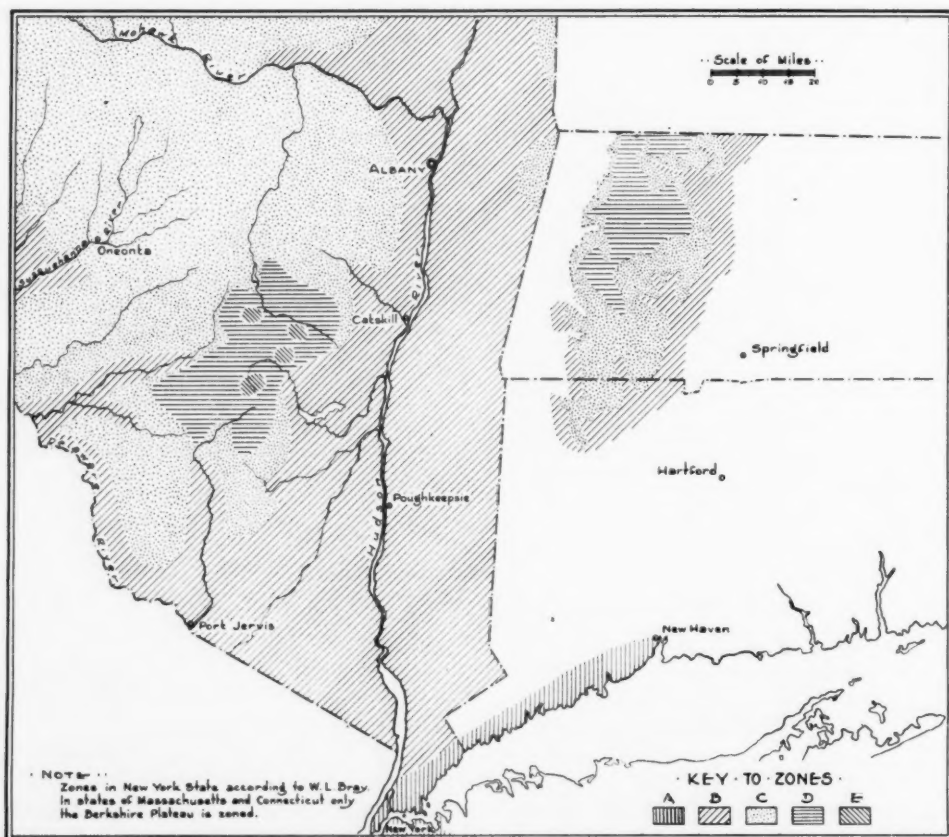


FIG. 5. Outline map of southeastern New York and adjacent New England, showing the location of zones A, B, C, D, and E.

In view of the divergence of opinion and lack of uniformity concerning nomenclature and concepts in European and American vegetation science and ecology, and furthermore in consideration of the lack of satisfactory correlation between the various classifications, the author does not in any case wish to assign the units used in this study to places in the current *a priori* systems.

ZONE C ON THE PLATEAU: THE BLANDFORD AREA

This region is named for the township of Blandford, where characteristic vegetation is well developed. Aside from the small acreage occupied by villages, farms, and gardens, the vegetation of the Blandford uplands can be readily segregated into a comparatively small number of distinct types. These may be listed and characterized as follows:

- I. Grasslands. All are anthropogenic. They occupy about 25 percent of the total land surface, and may occur on all upland sites, glacial streamside terraces, summits, and slopes of hills. *Anthoxanthum odoratum*, *Dactylis glomerata*, *Phleum pratense*, and *Poa pratensis* are the most abundant species. Four major communities are distinguished.
 - A. Tilled lands: the corn fields. These produce the silage for winter cattle feed, and possess a distinct assemblage of characteristic weeds. If abandoned for corn and mowed annually, the vegetation will become replaced in about five years by that of a typical meadow.
 - B. Mowed lands: the meadows. The herbaceous growth is cut annually for hay, usually in August. These fields occupy about 5 percent of the total Area. In general, due to lack of fertilization and artificial reseeding, the grass crop is of relatively low value. In early summer these fields usually present masses of pure color, due mainly to the local abundance of *Erigeron pulchellus*, *Chrysanthemum leucanthemum*, *Hieracium aurantiacum*, and *H. canadense*. *Rudbeckia hirta* appears later in the summer but is never as common as the preceding species. The vegetation of the mowed meadows is also characterized by the absence of many herbs elsewhere present, especially species of *Solidago*.
 - C. Grazed lands: the pastures. These lands, even under relatively intensive grazing, tend to be invaded by woody vegetation. The typical pasture is a close cropped sward, broken by the invading shrubs and trees of the next stage of evolution, the low juniper, *Juniperus communis* var. *depressa*, and white pine being the most successful. Pastures at present occupy 10 to 15 percent of the total area.
 - D. The unutilized grasslands. A strictly herbaceous community appears on corn fields, meadows, and pastures, when these sites are completely and abruptly abandoned. Such a community possesses many characteristic indicator species not found in other groupings, among which may be mentioned *Solidago rugosa*, *S. graminifolia*, *Gentiana andrewsii*, *G. crinita*, *Lilium philadelphicum*, *L. canadense*, and *Aster* spp. This grassland is ephemeral, and is invaded the same season or within a few years by woody species.
- II. Woody vegetation. All types are anthropogenic; no virgin communities have been found. Further discussion in this paper will be restricted to these types.
 - A. The Blandford Tree and Shrub Community of Old Fields. This segregate comprises a large number of species and exists in a great number of variations, the latter due essentially to priority of invasion and chance distribution rather than to an actual correlation with habitat factors.
 - B. The Blandford Summit Community. This is a unique forest type found very locally on a few of the more exposed hill tops. The stations may be considered as outliers of the oak and hickory forests of southern New England.
 - C. The Blandford Forest Herb Community. This segregate is almost entirely herbaceous, complex floristically, of many aspects, and existing more or less independently of the floristic nature of the tree community above it.

- D. The Blandford Northern Shrub Community. This assemblage of shrubs, dominated by striped maple (*Acer pennsylvanicum*), mountain maple (*Acer spicatum*), hobblebush (*Viburnum alnifolium*), and yew (*Taxus canadensis*) has distinct ecological unity.
- E. The Blandford Witch Hazel-Mountain Laurel Community. This grouping of shrubs is of austral floristic affinities.
- F. The Blandford Beech-Hemlock Community. This is the major forest tree community of the Area, completely anthropogenic today, and existing in an equilibrium with present conditions. It occurs largely as young even-aged stands on lands cut over several times and often temporarily pastured. This variable community is generally but not always accompanied by shrubs and by some aspect of the forest herb community, although in certain rare cases a typical grassland may be coexistent.

THE BLANDFORD TREE AND SHRUB COMMUNITY OF OLD FIELDS GENERAL CHARACTERISTICS

Agricultural lands that are not mowed, grazed, or tilled are invaded within a few years by woody plants of many species, of which gray birch and white pine are most abundant. The community is rich floristically and highly variable in physiognomy, structure, and in the number of species which may be locally dominant. It is best considered as a single aggregate because of its floristic unity and the ecological equivalence of its numerous aspects.

STRUCTURE OF THE COMMUNITY

Data to show the relative importance and distributional relations of the various species are presented in Table 2. The purpose of this table is not to give data of mathematical preciseness but to characterize the normal vegetation, which may then serve as a standard of comparison and reference for future studies. The figures in the tabulated descriptions are not arithmetical averages based on quadrat analyses; they represent estimations, made from precise observations on Frequency and Coverage at a large number of stations, and from the author's general knowledge of the vegetation acquired in the course of the study.

Here, and in other similar tables, the species of the community are characterized with reference to two features which are designated, respectively, as Presence and Coverage-when-present. The method thus adopted is similar to that employed by Nichols (1918) in describing the occurrence of herbs in certain forest types of Cape Breton Island. Furthermore, the two concepts are analogous to those of Quantity and Sociability, as applied in several recent publications of the S. I. G. M. A. at Montpellier.

Presence, as defined by Braun-Blanquet (1932:52) is "the more or less persistent occurrence of a species in all the stands of a certain plant community." In this paper, the term Presence is used to designate the relative occurrence of a plant in the stands of a specific community within an Area. For purposes of adequate comparison, all stands studied were about 5 acres

(2 hectares) in extent. Five percentages of Presence are recognized, 90, 70, 50, 30, and 10 percent.

The second concept is used to express the relative Coverage (as used by Cain, 1932) at those times when a species is present, this Coverage-when-present being independent both of its degree of Presence, and of its Abundance (number of individuals) and Density (average area of individuals). Three principal degrees of Coverage are recognized: (1) that varying between 100 and 66 percent; (2) that between 66 and 33 percent; and (3) that between 33 and 1 percent. An additional category of 1 percent to 0 is adopted, inasmuch as certain species are typically of very low Abundance. In general, the Coverage exhibited by any one species is not constant for all stands in which it occurs. This variation is recognized in Tables 2 to 10, inclusive, where the figures at the right represent the occurrence of a species in the four Coverage classes, in relation only to the total number of times that it exhibits Presence. The symbol “+” indicates that at least one record has been made of the species occurring in the class; “—” indicates a reasonable certainty that the species does not develop that particular Coverage.

The size of the stands adopted for expressions of Coverage-when-present is different from that uniformly adopted for Presence, and moreover differs for the different communities discussed in this paper. In every case the size of the stands has been so chosen as to give the maximum distribution of the species among the different Coverage classes. A stand relatively smaller in size would place a majority of the species in the higher Coverage classes; a larger stand would place them all in the lower classes.

TABLE 2. Presence and Coverage-when-present of the species of the Blandford Tree and Shrub Community of Old Fields. Figures for Presence refer to stands of 5 acres (2 hectares); those for Coverage-when-present refer to stands of ¼ acre (10 ares).

	Coverage			
	100-66 Percent	66-33 Percent	33-1 Percent	1-0 Percent
Presence of 90 percent:				
<i>Pinus strobus</i>	50	50	+	
<i>Betula populifolia</i>	50	50	+	
<i>Spiraea latifolia</i>	20	40	40	
<i>Spiraea tomentosa</i>	20	40	40	
<i>Rhus typhina</i>	10	40	50	
<i>Vaccinium corymbosum</i>	+	50	50	
<i>Acer rubrum</i>	+	25	75	
<i>Alnus incana</i>	+	10	90	
<i>Acer saccharum</i>	+	+	100	
<i>Prunus virginiana</i>	—	+	100	
<i>Rubus hispidus</i>	—	+	100	
<i>Fraxinus americana</i>	—		100	
<i>Pyrus malus</i>	—		100	
<i>Quercus borealis</i> Michx. ¹	—		100	
Presence of 70 percent:				
<i>Populus tremuloides</i>	5	5	90	
<i>Gaylussacia baccata</i>	—	10	90	
<i>Potentilla fruticosa</i>	—	10	90	
<i>Rubus allegheniensis</i>	—	10	90	
<i>Vaccinium pennsylvanicum</i>	—	10	90	

¹ The variety *maxima* (Marsh.) Sarg. is the typical form on the Berkshire plateau.

	Coverage			
	100-66 Percent	66-33 Percent	33-1 Percent	1-0 Percent
<i>Ilex verticillata</i>	—	+	100	
<i>Lyonia ligustrina</i>	—	+	100	
<i>Pyrus melanocarpa</i>	—	+	100	
<i>Dierzella lonicera</i>	—		100	
<i>Salix cordata</i>	—		100	
<i>Salix discolor</i>	—		100	
<i>Salix rostrata</i>	—		100	
<i>Viburnum cassinoides</i>	—		100	
<i>Viburnum dentatum</i>	—		100	
Presence of 50 percent:				
<i>Larix laricina</i>	25	50	25	
<i>Prunus pennsylvanica</i>	5	5	90	
<i>Kalmia latifolia</i>	+	20	80	
<i>Juniperus communis</i> var. <i>depressa</i>		10	90	
<i>Rubus idaeus</i> var. <i>aculeatissimus</i>		10	90	
<i>Tsuga canadensis</i>		10	90	
<i>Fagus grandifolia</i>	—		100	
<i>Rhododendron canescens</i>	—		100	
<i>Rhus toxicodendron</i>	—		100	
<i>Rubus odoratus</i>	—		100	
Presence of 30 percent:				
<i>Betula lutea</i>	10	15	75	
<i>Kalmia angustifolia</i>		5	95	
<i>Crataegus</i> spp.		+	100	
<i>Corylus rostrata</i>	—		100	
<i>Psedera quinquefolia</i>	—		100	
<i>Vaccinium vacillans</i>	—		100	
<i>Amelanchier canadensis</i>	—			100
<i>Cornus alternifolia</i>	—			100
<i>Nemopanthus mucronata</i>	—			100
<i>Sambucus canadensis</i>	—			100
<i>Sambucus racemosa</i>	—			100
<i>Viburnum acerifolium</i>	—			100
Presence of 10 percent:				
<i>Populus grandidentata</i>	—		100	
<i>Viburnum opulus</i> var. <i>americanum</i>	—		100	
<i>Lonicera caerulea</i> var. <i>villosa</i>	—			100
<i>Pyrus americana</i>	—			100
<i>Salix humilis</i>	—			100
<i>Ulmus americana</i>	—			100
<i>Vaccinium atrococcum</i>	—			100
<i>Viburnum lentago</i>	—			100

SOCIOGENETICS

Factors of priority of invasion, proximity to sources of seed, difficulties of establishment in a dense turf, colonization following establishment, and selective browsing by dairy cattle all affect to a marked degree the floristic composition and structure of the vegetation of abandoned meadows, pastures, and tilled fields. Such factors in many cases are to be interpreted as coincident or fortuitous, and existing vegetation is often therefore not the predictable result of ecological conditions.

The community is temporary, and is destined under natural conditions to give way within a relatively few years to the regional forest. One exception to the rapidity of change occurs in those cases where the long-lived white pine is dominant.

There is a definite tendency for many of the trees and shrubs of this aggregation to develop in more or less pure stands. These are undoubtedly the most satisfactory units of vegetation for future detailed investigation, and further discussions will be confined to the most important.

THE WHITE PINE COMMUNITY

The abundance and economic importance of white pine has led to the inclusion of the Blandford area by various authors in the so-called "white pine region" of central New England, which region is, however, by no means uniform in its vegetation. The present prevalence of white pine on the Plateau is due to a readily recognizable train of events: the progressive decrease of grazing in pastures and their gradual abandonment. Browsing by stock, unless very intensive, restricts the development of the hardwoods only and favors the pine to a stage where it is freed from competition with other species. To a certain extent, this tree may appear so abundantly that pure stands of straight-boled trees are developing which are sufficiently dense to eliminate the previous pasture vegetation. On the basis of extended field observations, however, it is doubtful if the number of localities in which such types are developing is sufficiently large to promise for the future the dense pure stands now maturing. The condition is related to the present outright abandonment of farm lands, with the resultant rapid invasion of deciduous-leaved species.

The time at which undergrowth in the pine forest first appears depends apparently less on the actual age of the timber than on the site quality, the density of the stand, and the degree of decomposition of the litter. Under older trees a large number of species are found, mainly those of the forest herb community, occurring in approximately the same degree of abundance as they do in other forests, with a few important exceptions. *Rubus hispidus*, *Lycopodium complanatum*, *Maianthemum canadense*, and *Gaultheria procumbens* are conspicuously more abundant than in the general upland forests. *Cypripedium acaule*, although always infrequent, is more or less confined to situations below pine, while *Vaccinium pennsylvanicum*, otherwise a pasture shrub, is common in the more open stands.

A few examples have been recorded where a distinct grassland community occurs under large old trees. Such a condition apparently arises by repeated destruction of the underbrush by fire, cutting, or especially by long-continued grazing. If this grassland is perpetuated, the old trees will eventually pass out of existence and the herbs will then become the dominant vegetation. On the other hand, cessation from disturbance for several years permits the establishment of large numbers of pine seedlings, which, if they mature, will form a second even-aged pine forest. Such a cycle of events should be considered when attempting to account for the large areas of pine known to have existed in some townships at the time of first settlement.

By nature, pure stands of pine on the Plateau are entirely unigenerational in character. If human interference were completely eliminated, they would

eventually become replaced and the community would disappear. Lumbering and cutting only hastens the change, since suppressed individuals of slower-growing tolerant species and an advance reproduction of other trees is usually present on the floor of any stand which is large enough to cut. Consequently, unless planting and selection are practiced, or new areas are first pastured and then progressively abandoned, the designation of "white pine region" in respect to the Plateau will soon be a matter of little more than historical interest. Seedlings of aspen (*Populus tremuloides*), fire cherry (*Prunus pennsylvanica*), paper birch (*Betula alba* var. *papyrifera*), and tamarack (*Larix laricina*) have never been observed below white pine; white pine seedlings themselves are normally absent, becoming established only in natural or artificial openings. Normally these stands are succeeded by the beech-hemlock community, the exact aspect of which depends largely upon priority of invasion.

THE GRAY BIRCH COMMUNITY

This phase, dominated by *Betula populifolia*, is one of the characteristic features of the landscape in the Blandford area, and is of phytosociological interest in that the natural understory is a grassland community, very closely related to that of pastures and meadows. Evolution advances toward any of several phases of the old field community, especially that of white pine, or directly to the beech-hemlock community. Succession proceeds rapidly, not only because of the openness of the canopy, but because the birch is very short-lived, averaging 30 to 60 years of age.

THE TAMARACK COMMUNITY

The position of the tamarack is of unusual interest. Here, as also in the Savoy area, this northern tree, customarily regarded as characteristic of swampy and boggy areas, is found in a wide variety of habitats, apparently being limited in its distribution primarily by one feature, its great intolerance. Tamarack must be considered an integral member of the old field community. Although it may be correlated with wet or seasonally moist habitats, where it may be abundant, it is impossible at present to attribute to it any indicator value of soil conditions.

Tamarack appears in varying degrees of abundance in mixture with a large number of species. It seems to be particularly susceptible to a leaf injury caused by the larch case-bearer (*Coleophora laricella* Hbn.). In late spring, the rusty trees stand out conspicuously in the pasture singly and in small groups. Younger individuals usually survive; the older ones are eventually killed, and consequently it is rare that trees above 6 or 8 inches in diameter and 35 feet in height are found.

In a pure dense colony of tamarack, secondary vegetation is remarkably scanty. In more open groups a grassland may be well defined. Customarily the stand is not pure and, with the gradual elimination of the tamarack, other species assume dominance and evolution progresses more or less rapidly to some phase of the beech-hemlock community.

THE ASPEN COMMUNITY

This aspect is of interest only as the local representative of the widespread aspen stands of the Adirondacks and the country to the north and west, where it is one of the commonest types following fires. On the Plateau aspens frequently occur in small groups of 50 to 200 trees, where they seldom attain a diameter of more than 6 inches and a height of 20 to 25 feet before succumbing to diseases and accidents. Grassland species invariably are found below the canopy, and these may be perpetuated by grazing. The stand is readily invaded by trees and shrubs, especially white pine, and evolution advances rapidly to various phases of the old field community.

OTHER COMMUNITIES IN WHICH OLD FIELD SPECIES PREDOMINATE

Certain habitats other than old fields and pastures, namely poorly drained mineral soils, lake shores, stream banks, trail sides, and hill tops, bear vegetation which, on floristic grounds, is closely related to the old field community. With few exceptions, the important trees and shrubs of such sites are common also on upland pastures but absent in the mature upland forests.

Thickets of alder (*Alnus incana*) are by far the most frequent type of vegetation on poorly drained soils. This species is usually more or less mixed with red maple (*Acer rubrum*) (a tree which is characteristic of the next stage of succession on these sites), although the density of some alder thickets may temporarily inhibit all advance reproduction both of red maple and other species. The alder is quite aggressive and will usually invade poorly drained sites following destruction of or disturbance to the vegetation. It will also appear on and dominate such sites as previously bore upland vegetation, but which, through man's activities, are now poorly drained continuously or seasonally. Other species commonly found on swampy lands are *Carpinus caroliniana*, *Lyonia ligustrina*, *Nemopanthus mucronata*, *Ilex verticillata*, *Spiraea tomentosa*, *S. latifolia*, *Ulmus americana*, *Vaccinium corymbosum*, *Viburnum cassinoides*, and *V. dentatum*.

In a narrow strip along many lake shores, the additional side illumination may be the factor that permits the persistence of many species, some of which are common in swamps, and all of which occur in old fields. The following are found in mature forests along lake shores: *Alnus incana*, *Betula populifolia*, *B. alba* var. *papyrifera*, *Ilex verticillata*, *Lyonia ligustrina*, *Nemopanthus mucronata*, *Prunus virginiana*, *Pyrus melanocarpa*, *Rhus typhina*, *Rubus* spp., *Spiraea latifolia*, *S. tomentosa*, *Vaccinium corymbosum*, *Viburnum cassinoides*, *V. dentatum*. Stream banks are apparently a similar but less extreme kind of habitat. Alder is the shrub most frequently found, but many others also occur.

Slight differences in ecological conditions caused by the removal of vegetation for a trail or path may be sufficient to permit the establishment or persistence of occasional intolerant old-field species. For this reason the

character of the closed forest cannot always be judged unless it be traversed without a trail.

Many of the hill tops have been used for pasturing, but with their abandonment evolution advances very slowly toward a closed forest. Shrub stages and even herbaceous stages show definite evidence of persistence on the more exposed summits. In those cases where the forest was never wholly destroyed, or where a tree cover at present exists, certain trees and shrubs may be found which do not occur on the slopes below, and which only reappear in abandoned fields. These include: *Alnus incana*, *Amelanchier canadensis*, *Betula alba* var. *papyrifera*, *Betula populifolia*, *Carpinus caroliniana*, *Gaylussacia baccata*, *Lyonia ligustrina*, *Nemopanthus mucronata*, *Populus tremuloides*, *Prunus virginiana*, *Pyrus melanocarpa*, *Rhus typhina*, *Rubus* spp., *Spiraea latifolia*, *S. tomentosa*, *Ulmus americana*, *Vaccinium corymbosum*, *Vaccinium pennsylvanicum*, *Viburnum cassinoides*, and *Viburnum dentatum*.

Many of the more exposed tree-covered hill tops throughout the Area, particularly those which show evidence of pasturing in the past, are characterized by a very distinct bush form or krummholz-like type of growth, varying from 10 to 20 feet in height. Yellow birch, beech, sugar maple, and red maple are the species most often affected. At least in some cases, this ecological growth-form definitely comprises a stage which is temporary and which will be succeeded by a community floristically similar, but of tall straight-boled trees.

THE BLANDFORD SUMMIT COMMUNITY

On certain of the most exposed hill tops in the Blandford area, there is developed a very unique type of vegetation, floristically related to the forest communities of southern New England and correspondingly distinct from the generally distributed northern hardwood types of the vicinity. Only a half dozen examples of this community, varying from one to four acres in extent, have been studied; it is doubtful if twice this number are in existence. So perfect is the correlation with topographic features of a monadnock type that following the discovery of the first, others were postulated from a study of the U. S. Geological Survey topographic maps and their existence later verified. These isolated islands, predominantly oak and hickory, do not occur at any definite altitude. They bear no evident relation to steepness of slope; neither would it appear that their development is determined by local variations in soil moisture, kind or depth of soil, or presence of rock outcrops. In several instances, the community descends below the summits on the east and south sides.

Great variation exists in degree of exposure, depth of soil, and floristic composition of the vegetation of these hill tops. The community is characterized by the predominance of certain trees, such as red oak (*Quercus borealis* Michx.) and hop hornbeam (*Ostrya virginiana*), neither of which is ever

abundant in the surrounding forests, and shagbark hickory (*Carya ovata*), bitternut hickory (*Carya cordiformis*), white oak (*Quercus alba*), and chestnut oak (*Quercus montana* Willd.), all of which are practically absent on the adjoining slopes below. At any one station one or two of these species predominate; the others, if found at all, are infrequent. The presence of hop hornbeam is one of the best indicators of the hill-top environment, although it is on the margins of the community where its best regional development is attained, here reaching a diameter of 18 inches. Many trees and shrubs common in old fields also occur on the summits, such as *Prunus virginiana*, *Rubus* spp., *Spiraea* spp., *Gaylussacia baccata*, *Amelanchier canadensis*, and *Carpinus caroliniana*. These communities where best developed are also characterized by the absence of certain trees found in the immediate vicinity, namely hemlock, beech, yellow birch, sugar maple, basswood (*Tilia americana*), white pine, paper birch, and black birch, (*Betula lenta*), sometimes also gray birch and red maple. White ash (*Fraxinus americana*) may be present as an unimportant constituent.

On soils of appreciable depth the trees are small, often not above 25 feet in height, and clear of branches on the lower half. This absence of lower branches on the trees, coupled with a poor development of shrubs below, permits an unobstructed view through the stand which is at complete variance with the appearance of the dense vegetation on the lower slopes of the same hills. A turf of low sedges, forming a dense ground cover of a type not found elsewhere in the Area, may develop on such sites. *Aspidium marginale*, while occurring regularly in the upland forests, here becomes more frequent though not common. Other than this fern, there are no conspicuous small plants characterizing the ground cover. Seedlings of sugar maple, red maple, oak, ash, and white pine are sometimes found, but at least in some cases do not appear destined to succeed the present forest.

Where the soil is thin and rock outcrops are frequent, the trees are often widely scattered, with red oak, hop hornbeam, and occasionally red maple best able to survive. Such individuals may be only 15 feet high and may assume a growth form found only on such summits, in which excessive branching has removed all resemblance to a tree. When these die and fall, their disintegration is very slow, and branches remain on the ground for many years, devoid of bark, bleached, and with no evidence of decay.

All known examples of the community have suffered much from cutting and grazing, and it does not seem justifiable from existing evidence to discuss their stability. In some cases there are indications of invasion by species of the northern hardwood type; in other cases, oaks and hickories are succeeding the present stand. It is likely that disturbances due to cutting and grazing have extended the areas of these summit communities at the expense of the northern hardwoods, which again encroach during prolonged protection. Whether or not the entire vegetation may be replaced by northern hardwoods

is hypothetical. Considering that similar communities of the southern Taconics are permanent, those of the southern Berkshire plateau are probably so also, at least in the more extreme examples.

These summit communities might be considered on first thought as the advance guards of a northward migration of the deciduous forest, such as might still be occurring subsequent to the last glacial period, and the pure stands and floristic paucity might be interpreted as due to incomplete introduction of the southern species. Nevertheless, in the reconnaissance of the Deerfield River area where presumably all the southern species have equal chances of immigration, the same varying dominance by a single species was noted. Hickory, white oak, chestnut oak, and bitternut may be individually abundant at the lower elevations over 5 or 10 square miles at a time, while various others may be relatively infrequent. This condition cannot as yet be linked with existing causal factors.

THE BLANDFORD FOREST HERB COMMUNITY

The herb stratum community of the Blandford forests is well developed in 90 percent or more of the mature stands. It is entirely absent only from dense early growth of beech, sugar maple, hemlock, and white pine, and in situations where yew, hobblebush, or laurel (*Kalmia latifolia*) grow profusely. The forest herb community is relatively independent of the floristic nature of the tree canopy above it, which here is best considered an environmental factor rather than as part of the same community. The aggregation is composed of a large number of species, mainly boreal, of which none are of outstanding abundance. They are all capable of surviving under a dense arboreal or shrubby canopy, and a majority are restricted to this type of habitat. A few, however, like *Aspidium spinulosum*, *Aralia nudicaulis*, *Maianthemum canadense*, and *Mitchella repens*, are found in a variety of situations in this and adjoining regions. Even though among the predominants here, they have therefore a very low Fidelity (that is, the limitation of a species to a definite plant community).

On the whole, the herbs of meadows, open woods, and of the oak forests of southern New England are absent. To some extent therefore, this association may be further characterized by the absence of predominant species of those communities, to wit: all grasses (except *Brachyelytrum erectum*); such presumably intolerant species as *Aster* spp. (except *A. divaricatus*, and *A. acuminatus*), *Desmodium* spp., *Hieracium* spp., *Lysimachia quadrifolia*, and *Solidago* spp. (except *S. caesia*); and many spring-flowering herbs typical of the deciduous forest to the south and west, as *Sanguinaria*, *Podophyllum*, *Chelidonium*, *Claytonia*, *Ientaria*, *Dicentra*, and *Erythronium*.

As characterized by its predominant species, this herb layer, as well as the associated tree layer, is strikingly similar to that of other northern hardwood areas, as described by Hill (1923) for the Penobscot Bay region of Maine, by Nichols (1918) for Cape Breton island, Nova Scotia, by Adams

et al. (1920) for the Adirondacks in the vicinity of Mt. Marcy, and by Hough (1936) for northwestern Pennsylvania. In the case of the glacial podzol Kennan soils of Wisconsin, Wilde (1934) has found that "the moderately acid phase of these soils is characterized by reactions of pH 5.5 to 6.5, with extremes of pH 5.0 to 6.8, and supports an association of minimiacidophilous plants, such as maidenhair fern, sweet cicely, meadow rue, water leaf, hog peanut, vetchling, and leather wood. The strongly acid phase of the same types is characterized by an acidity of pH 4.0 to 5.0 with extremes of pH 3.8 and 5.5, and supports an association of acidophilous plants, such as clintonia, clubmoss species, wild lily-of-the-valley, bunch berry, partridge berry, twin flower, and creeping yew." The affinities of the Blandford community to the latter is obvious.

Only one species in this association, *Polypodium vulgare*, can be said to be sociologically and ecologically distinct. This fern is one of the most characteristic plants on large rocks and boulders within the forest, less often on rocks exposed to sunlight, where it develops a fibrous mat up to three inches in thickness, composed of rhizomes, roots, and accumulated debris. With sufficient development of the mat, other herbs and even trees and shrubs appear, but ordinarily only the fern is present.

In Table 3 are listed one hundred of the plants characteristic of this herb layer of the Blandford forests. The list is necessarily incomplete; the sociological status of certain rare plants is not yet known, and a few species may have been overlooked. One difficulty in giving a satisfactory picture of the structure of this community is due to that fact that many pasture plants, particularly *Dicksonia punctilobula*, may become more or less temporarily established in openings in the forest. The floristic variations of the community thus developed differ greatly in size, abundance, and permanency.

Vitality, as used by Braun-Blanquet (1932), refers to the degree to which a plant prospers in a certain plant community, as expressed especially by the vigor of growth, flowering, fruiting, and germination. Of the species listed in Table 3, the following, although fruiting in the closed forest, never develop as luxuriantly as on the margins of stands and in thinned woods: *Asplenium felix-femina*, *Aster acuminatus*, *Aster divaricatus*, *Botrychium virginianum*, *Dicksonia punctilobula*, *Equisetum arvense*, *Eupatorium urticacifolium*, *Laportea canadensis*, *Onoclea sensibilis*, *Osmunda cinnamomea*, *O. claytoniana*, *O. regalis*, *Pteris aquilina*, *Solidago caesia*, *Trillium erectum*, and *T. undulatum*. There is another group of species, which, although constant in the closed forest, do not complete their life cycle except in open woods and pastures: *Amphicarpa monoica*, *Corydalis sempervirens*, *Geum canadense*, *Lysimachia quadrifolia*, *Polygonatum biflorum*, *Prenanthes trifoliolata*, *Pyrola americana*, *Smilacina racemosa*, *Thalictrum dioicum*, and *Veronica officinalis*. The shrubs *Cornus alternifolia*, *Rhododendron canescens*, and *Sambucus racemosa* at higher elevations, belong in this category. When any of these species occur in the Savoy area, their development is similar to that reported above.

TABLE 3. Presence and Coverage-when-present of the species of the Blandford Forest Herb Community. Figures for Presence refer to stands of 5 acres (2 hectares); those for Coverage-when-present refer to stands of one are (100 square meters).

	Coverage			
	100-66 Percent	66-33 Percent	33-1 Percent	1-0 Percent
Presence of 90 percent:				
<i>Aralia nudicaulis</i>	5	50	45	
<i>Aspidium spinulosum</i>	5	50	45	
<i>Maianthemum canadense</i>	5	50	45	
<i>Mitchella repens</i>	5	50	45	
<i>Tiarella cordifolia</i>	5	50	45	
<i>Acer saccharum</i>	+	50	50	
<i>Polystichum acrostichoides</i>	+	25	75	
<i>Tsuga canadensis</i>	+	10	90	
<i>Acer saccharinum</i>				100
<i>Fraxinus americana</i>				100
<i>Quercus borealis</i> Michx.				100
Presence of 70 percent:				
<i>Aster divaricatus</i>	+	75	25	
<i>Aspidium noveboracense</i>		50	50	
<i>Eupatorium urticaefolium</i>		50	50	
<i>Brachyelytrum erectum</i>		25	75	
<i>Oxalis acetosella</i>		10	90	
<i>Gaultheria procumbens</i>		10	90	
<i>Polygonatum biflorum</i>		10	90	
<i>Smilacina racemosa</i>		10	90	
<i>Galium triflorum</i>		10	90	
<i>Viola</i> spp.		10	90	
<i>Tridentalis americana</i>			100	+
<i>Pyrola americana</i>			100	+
<i>Prunus serotina</i>	—			100
Presence of 50 percent:				
<i>Polypodium vulgare</i>	75	25	+	
<i>Dicksonia punctilobula</i>	50	50	+	
<i>Osmunda claytoniana</i>	10	80	10	
<i>Aster acuminatus</i>	10	80	10	
<i>Osmunda cinnamomea</i>	10	80	10	
<i>Epifagus virginiana</i>		10	90	
<i>Oakesia sessilifolia</i>		10	90	
<i>Lycopodium clavatum</i>		10	90	
<i>Lycopodium complanatum</i>		10	90	
<i>Lycopodium lucidulum</i>		10	90	
<i>Clintonia borealis</i>		10	90	
<i>Amphicarpa monoica</i>	+	+	100	
<i>Lycopodium obscurum</i>		+	100	
<i>Collinsonia canadensis</i>		+	100	
<i>Hepatica triloba</i>		+	100	
<i>Medeola virginiana</i>		+	100	
<i>Hydrocotyle americana</i>		+	100	
<i>Pyrola elliptica</i>			100	
<i>Arisaema triphyllum</i>	—		100	
<i>Monotropa uniflora</i>	—		100	
<i>Phegopteris polypodioides</i>	—		100	
<i>Solidago caesia</i>	—		100	
<i>Actaea alba</i>	—	—		100
<i>Actaea rubra</i>	—	—		100
<i>Epipactis pubescens</i>	—			100
<i>Fagus grandifolia</i>	—			100
<i>Prenanthes trifoliolata</i> (?)	—			100
Presence of 30 percent:				
<i>Coptis trifolia</i>		10	90	
<i>Cornus canadensis</i>		10	90	

	Coverage			
	100-66 Percent	66-33 Percent	33-1 Percent	1-0 Percent
<i>Onoclea sensibilis</i>		10	90	
<i>Pilea pumila</i>		10	90	
<i>Asarum canadense</i>	—	+	100	
<i>Asplenium filix-femina</i>	—	+	100	
<i>Chimaphila umbellata</i>	—	+	100	
<i>Circaea alpina</i>	—	+	100	
<i>Geum canadense</i>	—	+	100	
<i>Laportea canadensis</i>	—	+	100	
<i>Lycopodium annotinum</i>	—	+	100	
<i>Veronica officinalis</i>	—	+	100	
<i>Aralia racemosa</i>	—	—		100
<i>Aspidium marginale</i>	—	—		100
<i>Betula lutea</i>	—	—		100
<i>Botrychium virginianum</i>	—	—		100
<i>Mitella diphylla</i>	—	—		100
<i>Monotropa hypopitys</i>	—	—		100
Presence of 10 percent:				
<i>Pteris aquilina</i>	—	100		
<i>Adiantum pedatum</i>	+	50	50	
<i>Chiogenes hispidula</i>		10	90	
<i>Equisetum arvense</i>		10	90	
<i>Osmunda regalis</i>		10	90	
<i>Corydalis sempervirens</i>		10	90	
<i>Moneses uniflora</i>	—	10	90	
<i>Veratrum viride</i>	—	10	90	
<i>Caulophyllum thalictroides</i>		+	100	
<i>Impatiens biflora</i>		+	100	
<i>Thalictrum dioicum</i>		+	100	
<i>Asplenium acrostichoides</i>	—		100	
<i>Aspidium cristatum</i>	—		100	
<i>Cystopteris fragilis</i>	—		100	
<i>Galium lanceolatum</i>	—		100	
<i>Hydrophyllum virginianum</i>	—		100	
<i>Lysimachia quadrifolia</i>	—		100	
<i>Pyrola chlorantha</i>	—		100	
<i>Solidago latifolia</i>	—		100	
<i>Cypripedium acaule</i>			10	90
<i>Osmorhiza claytoni</i>			+	100
<i>Sanicula marilandica</i>			+	100
<i>Circaea lutetiana</i>	—	—		100
<i>Corallorhiza maculata</i>	—	—		100
<i>Epigaea repens</i>	—	—		100
<i>Panax trifolium</i>	—	—		100
<i>Pedicularis canadensis</i>	—	—		100
<i>Smilax herbacea</i>	—	—		100
<i>Streptopus amplexifolius</i>	—	—		100
<i>Streptopus roseus</i>	—	—		100
<i>Trillium erectum</i>	—	—		100
<i>Trillium undulatum</i>	—	—		100

The concept of Fidelity has reference to the more or less rigid limitation of a species to a definite plant community. The following species, although constant within the forest, are much more abundant on roadsides, exposed areas, and fields: *Amphicarpa monoica*, *Asplenium acrostichoides*, *Asplenium filix-femina*, *Botrychium virginianum*, *Corydalis sempervirens*, *Dicksonia punctilobula*, *Equisetum arvense*, *Laportea canadensis*, *Lycopodium clavatum*, *L. complanatum*, *Lysimachia quadrifolia*, *Osmunda claytoniana*, *Prenanthes*

trifoliolata, *Pteris aquilina*, *Thalictrum dioicum*, *Veronica officinalis*. Within the closed forest, certain sites are frequently more moist, and in such places the following species become more abundant: *Arisaema triphyllum*, *Coptis trifolia*, *Cystopteris fragilis*, *Hydrocotyle americana*, *Impatiens biflora*, *Onoclea sensibilis*, *Osmunda claytoniana*, *O. cinnamomea*, *O. regalis*, *Pilea pumila*, and *Veratrum viride*. When these species occur in the Savoy area, their distribution is similar.

THE BLANDFORD WITCH HAZEL-MOUNTAIN LAUREL COMMUNITY

Two shrub communities are restricted to the forests of the Blandford area, namely, the Witch Hazel-Mountain Laurel Community and the Northern Shrub Community. Since in many places these two are telescoped into one, their separation here is partially arbitrary, being based in a large measure upon the nature of related communities without the Area. Of the two aggregations, the latter is northern in its general distribution, while the former is widely distributed southward.

This community, as well as that next to be described, is remarkable for its floristic paucity. Other than the two dominants already named, there are only five species of significant Presence, all of very low Coverage, while the many shrubs and small trees of old fields are characteristically absent. Data for Presence and Coverage-when-present of the species are given in Table 4.

TABLE 4. Presence and Coverage-when-present of the species of the Blandford Witch Hazel-Mountain Laurel Community. Figures for Presence refer to stands of 5 acres (2 hectares); those for Coverage-when-present refer to stands of $\frac{1}{4}$ acre (1,000 square meters).

	Coverage			
	100-66 Percent	Percent 66-33	33-1 Percent	1-0 Percent
Presence of 90 percent:				
<i>Kalmia latifolia</i>	10	25	65	
<i>Hamamelis virginiana</i>	5	15	80	
Presence of 70 percent:				
<i>Castanea dentata</i> ¹			+	100
Presence of 50 percent:				
<i>Cornus alternifolia</i>				100
<i>Lonicera canadensis</i>				100
Presence of 30 percent:				
<i>Rhododendron canescens</i>				100
<i>Viburnum acerifolium</i>				100

¹ *Castanea dentata* is not to be considered as a transgressive, as shoots of this species are blighted before they attain the size of a tree.

Of the two shrub communities of the Area, the Witch Hazel-Mountain Laurel is the more xeric, being of most frequent occurrence on south-facing slopes, summits, and disturbed cut-over lands. There is much intergradation, however, and about 25 percent of the forest now contains various mixtures of both groups. It is possible that disturbances during the last century have served to segregate these two to a greater extent than had originally

existed. Relatively xeric and well-lighted habitats favorable to laurel have been created in many places through continual cutting. At the same time uniformly mesic and well-shaded habitats have been produced under even-aged stands that are unfavorable to its development.

Optimum conditions for this community are to be found under tree canopies of medium density where a state of temporary equilibrium is reached, and where the community is characterized by a relatively constant structure. Under such conditions, the laurel forms a woody tangle of 100 percent Coverage, the plants varying from 2½ to 7 feet high, but flat-topped for any one site. Plants of the witch hazel (*Hamamelis virginiana*) occur at intervals of 15 to 25 feet, the stems rising above the surface of the laurel, and their branches meeting overhead at a total height of 8 to 15 feet, where a relatively thin layer of deciduous foliage forms a second complete cover. One of the conditions necessary for the establishment of such equilibrium is the absence of transgressives, that is, an advance reproduction of species destined to dominate the upper canopy. Seedlings of forest trees do not readily enter this closed community and, consequently, destruction of this layer is commonly resorted to in silvicultural practice. Such action may be carried to an extreme, when brambles invade the site and forest regeneration is again impaired. Under natural conditions, the optimum phase of the Witch Hazel-Mountain Laurel Community is not stable, due largely to the changes which occur in the upper canopy of overmature and uneven-aged forests. In virgin stands, optimum phases would probably exist only locally.

Witch hazel and mountain laurel are, above all others, the two commonest shrubs of the Blandford area. They are relatively similar in their ecological requirements. The former almost never occurs without the other, although it may be the more common along streamsides and in ravines. Mountain laurel, on the other hand, develops frequently in pure thickets, particularly on upper and south-facing slopes where it may form impenetrable tangles of woody growth in which, because of rooted decumbent branches, the individuals are not in evidence. Laurel does not attain the luxuriance of growth which it exhibits in the more open woodlands of the Taconics and other relatively austral regions.

THE BLANDFORD NORTHERN SHRUB COMMUNITY

This community, growing in more mesic situations than the preceding, is not as widely distributed and is found generally on north-facing slopes, in ravines, and on other favorable sites. In all probability, a large proportion of land now supporting young even-aged stands without distinct shrub layers will be invaded in the future by this northern community provided the stands are allowed to become overmature. The manner of occurrence of the species is presented in Table 5.

TABLE 5. Presence and Coverage-when-present of the species of the Blandford Northern Shrub Community. Figures for Presence refer to stands of 5 acres (2 hectares); those for Coverage-when-present refer to stands of $\frac{1}{4}$ acre (1,000 square meters).

	Coverage			
	100-66 Percent	66-33 Percent	33-1 Percent	1-0 Percent
Presence of 90 percent:				
<i>Viburnum alnifolium</i>	50	50	+	
<i>Acer pennsylvanicum</i>	50	50	+	
<i>Acer spicatum</i>	50	50	+	
Presence of 70 percent:				
<i>Cornus alternifolia</i>				100
<i>Lonicera canadensis</i>				100

The four important species, namely striped maple, mountain maple, hobblebush, and yew, are shrubs and shrubby trees which are very characteristic of the northern hardwood type of forest. All are common throughout the Area and apparently are very similar to one another in certain of their ecological requirements. In this region they are distinctly forest species, never found in old fields and quickly disappearing on destruction of the tree layer. The associated species, hazel (*Corylus rostrata*), alternate-leaved dogwood (*Cornus alternifolia*), and red-berried elder (*Sambucus racemosa*), are more abundant on the forest edge and along roadsides; all three flower and fruit only in such open situations. Fly honeysuckle (*Lonicera canadensis*) is essentially restricted to the forest, and is only occasionally seen in fruit.

Optimum conditions for the development of this community are attained only rarely and then under the uniform canopy of an even-aged closed forest. At such times, structural characteristics are most clearly evident in the layering within the community. For example, a dense growth of yew may cover the ground to a height of 18 to 30 inches, above which is an open tangled mass of hobblebush rising to a total of $2\frac{1}{2}$ to 4 feet. Unless the yew is absent, an herb layer is not present. In either case, conditions are unfavorable for tree reproduction. Mountain maple and striped maple are apparently ecological equivalents and, pure or in mixture, they form a distinct stratum with a complete coverage at a height of 15 to 20 feet above the ground, the plants themselves usually being 10 to 25 feet apart. Like the corresponding phase of the Witch Hazel-Mountain Laurel Community, this aspect is not stable and the uniform structure will disappear when the overlying canopy of trees becomes broken and irregular.

Both of the northern maples sprout prolifically from the stump. In some cases following clear-cutting, the stump sprouts of these species are the most aggressive and the most rapidly growing shoots. Consequently they may develop as dominants of the upper canopy, attaining heights of 30 feet and diameters of 6 to 8 inches. Pure stands which have arisen in this way have been found covering areas up to $\frac{1}{4}$ acre in extent. Tree reproduction of forest species in these stands is very effectively, although temporarily, inhibited, and no definite successional trends may be observed.

THE BLANDFORD BEECH-HEMLOCK COMMUNITY

GENERAL CHARACTERISTICS

The community thus designated is the regional forest tree community as developed in, and restricted in its occurrence to, the Blandford area. With beech, hemlock, sugar maple, and yellow birch as the most important species, it is the local representative of the upper canopy of the widely distributed northern hardwood forest of northeastern North America, and corresponds closely to the type in all its general features. It includes fully 90 percent of the forest stands in the Area, and varies greatly in composition from place to place, comprising in this respect a mosaic of variations directly the result of anthropic activities. At the present time, dense young even-aged stands prevail on all forest lands, very frequently being pure groupings of hemlock or beech. Such stands, usually 30 to 60 years of age, provide constant conditions over local areas that are favorable to the uniform development of the lower strata and are adaptable to detailed ecological investigations.

FLORISTICS AND STRUCTURE

The beech-hemlock community is composed of species predominantly northern in their general distribution; trees typical of the forests of the southern Appalachians and Ohio River valleys are notably absent. Although in ravines individuals occasionally attain heights of 75 feet and diameters of 18 inches, in general they average 30 to 50 feet in height and 9 to 12 inches in diameter. The community characteristically develops an entirely closed canopy, keeping the forest interior in dense shade unfavorable for lesser vegetation. Natural openings or grassy clearings are unknown. At least 50 percent of the stands possess definite shrub communities which usually vary in Coverage from 50 to 75 percent, rarely 100 percent. The frequent absence of shrub strata in dense growth is a temporary condition rather than a natural one for the site, and in virgin stands the condition would be much less prominent. Herbaceous strata occur in approximately 90 percent of the forests, being temporarily absent below young trees.

Data for Presence and Coverage-when-present for the tree species of this community are given in Table 6. Beech and hemlock form the bulk of the vegetation, with hard maple, yellow birch, red oak, red maple, and white ash locally abundant. When a few large paper birch or large-toothed aspen—the latter attaining heights of 75 feet and diameters of 18 inches—are found in the forest, they may be interpreted as having become established at a time of clear-cutting. Hop hornbeam, one of the characteristic under-trees of the eastern deciduous forest, is not sufficiently abundant in the Area to assume a definite role. It may attain a height of 30 feet and a diameter of 9 inches in young stands, but it is virtually absent in old dense forests. American hornbeam (*Carpinus caroliniana*) is occasionally found along streamsides and on hill tops, but was nowhere observed a member of the

forest. American elm (*Ulmus americana*) is infrequent both here and in the Savoy area. It occasionally occurs along brooks in young forests, but seedlings have never been found within the stands.

TABLE 6. Presence and Coverage-when-present of the species of the Blandford Beech-Hemlock Community. In this table, figures for Presence refer to stands of 5 acres (2 hectares); those for Coverage-when-present refer to stands of 2½ acres (1 hectare).

	Coverage			
	100-66 Percent	66-33 Percent	33-1 Percent	1-0 Percent
Presence of 90 percent:				
<i>Tsuga canadensis</i>	25	50	25	
<i>Fagus grandifolia</i>	25	50	25	
<i>Acer saccharum</i>	+	40	60	
<i>Betula lutea</i>	+	30	70	
<i>Quercus borealis</i> Michx.	+	30	70	
<i>Acer rubrum</i>	+	20	80	
<i>Fraxinus americana</i>		10	90	
<i>Betula alba</i> var. <i>papyrifera</i>			+	100
Presence of 70 percent:				
<i>Pinus strobus</i>	—	—	10	90
<i>Tilia americana</i>	—	—	+	100
<i>Prunus serotina</i>	—	—	+	100
Presence of 50 percent:				
<i>Betula lenta</i>	—		+	100
<i>Ostrya virginiana</i>	—	—		100
Presence of 30 percent:				
<i>Populus grandidentata</i>	—	—		100

THE STATUS OF HEMLOCK

A careful search was made for any ecologic peculiarities or edaphic and topographic affinities of the hemlock. In this connection, a study of aerial photographs¹ revealed it as abundant in certain ravines, but gave no indication of consistency in such distribution. The proportion of ravines bearing hemlock on the Plateau is not significantly greater than the proportion of upland areas. To account for the distinctive character of the vegetation of such sites it is not necessary to postulate any "post-climax" or "relict" status for this tree. In the first place, there are strong indications that lumbering tends to reduce the amount of hemlock in the forest where advance reproduction is not present, because of the very rapid early growth of subsequently appearing deciduous species. Ravines, because of their steep and rocky sides, are frequently less often cut over and the abundance of hemlock is due to natural development.

Nichols (1916:244) recognizes immunity from fire as a very important factor in the perpetuation of hemlock ravines in Connecticut, in addition to freedom from lumbering. This condition is certainly true for much of southern New England, where the forests in general are relatively dry, more open, and inflammable. In the Blandford area, however, fires are very un-

¹ Valuable information concerning the distribution of certain cover types may be obtained from study of the aerial survey of the State of Massachusetts, at the Institute of Geographical Exploration at Harvard University. These prints are on a scale of 1:30,000, taken with a Fairchild 5-lens camera from an altitude of 15,000 feet.

usual and uplands suffer little more than do the ravines. The inability of hemlock to cope with fire in this and similar types, mainly because of its shallow root system, has been commented upon by Nichols (1913b:211) in connection with the virgin Colebrook forest, and by Hough (1936) for the Tionesta region of Pennsylvania.

Brief reference should be made to the sociological status of hemlock as conceived by Weaver and Clements (1938:498). In their opinion, "the view that hemlock is properly a member of the deciduous forest runs counter to the rule as to the identity of life forms and has not taken sufficient account of the nature of relicts." At the present time no unusual peculiarities are known in the ecological requirements of hemlock, as it occurs on the Plateau, which would indicate that it deserves sociological distinction in any manner but by its life form. It is apparent that only by virtue of unconditional acceptance of the "rule"—whatever its arbitrary basis be—can such distinction be established. This interpretation for hemlock in the Blandford area has no reference to its status in other regions.

SOCIO-GENETICS

The community in several ways is remarkable for its great areal extent in the face of repeated disturbances. It is attained quite rapidly in the course of succession on all abandoned agricultural lands, except on exposed hill tops and on old fields bearing white pine. On forest land the community has persisted despite the extensive disturbances due to cutting for charcoal, firewood, and lumbering. The persistence is due not to the fact that destruction has been less violent in this Area than in others, but that there are no aggressive pioneer species to take control at times of destruction and to transform the community.

DEVELOPMENTAL TENDENCIES IN THE BLANDFORD FORESTS

Evolution within the undisturbed beech-hemlock forest is closely conditioned by the relative tolerance of the species. "Tolerance" is here used to refer to the ability of a plant to survive and develop under the complex of conditions existing below an upper canopy, of which deficient light and soil moisture are apparently the most important. Frothingham (1915:12), Toumey and Korstian (1937) and Zon and Graves (1911) have discussed the relative tolerance of the species which are dominant in the Blandford forests. Tolerance varies slightly according to general climatic conditions and consequently their findings should not and cannot be directly applied. Present investigations have shown that white pine is markedly intolerant, that red oak, red maple, black cherry (*Prunus serotina*), and white ash are capable of surviving as seedlings in relatively dense shade, and that sugar maple, beech, and hemlock are of greatest tolerance.

Sugar maple seedlings are very common in many of the forests, although nowhere do they form a dense ground cover. As a general rule, they are

about 4 inches in height, persisting but failing to develop further in the dense shade, and putting on significant growth only where the forest is open or the canopy broken. On the other hand, beech root-suckers (beech seedlings are rare) and hemlock seedlings tend to dominate the advance reproduction wherever present. This condition has been responsible for the present abundance of these two species in the Blandford area. It will favor their continued abundance in the future under existing methods of cutting, inasmuch as the stands are never allowed to become sufficiently overmature and open to permit the development of the less tolerant forest trees. On the other hand, selective thinning of young growth can easily upset this trend of events.

In those situations where a heavy advance reproduction of beech and hemlock is not present, regardless of the floristic composition of the upper canopy, selective cuttings favor the abundance of sugar maple, yellow birch, red oak, red maple, white ash, and black cherry in the order named. White pine may appear if the land is temporarily pastured.

With a general knowledge of the life histories of the important forest species, it is possible to postulate the train of events which would take place if artificial disturbances were completely eliminated. In the first place, the conditions for germination and development of tree species on the forest floor, as affected by the unbroken canopies of the existing stands, is extremely unfavorable. The species best suited to dominate the advance reproduction under such cover are hemlock and beech; and the naturally succeeding forest, whether or not the stand is pure or mixed hemlock-hardwood now, would very likely be dominated by one or the other, or less often by a mixture of the two. Furthermore, such species as sugar maple, red maple, ash, cherry, and red oak, the seedlings of which are customarily found persisting in closed forests, will become less abundant in the upper canopy than they are now; while other species, usually recognized as more or less intolerant, including yellow birch, paper birch, black birch, hop hornbeam, and white pine, will become greatly reduced in number and even locally absent.

Further changes will later occur in the forest which would affect both its structure and its composition and which would tend to bring about a relatively permanent state of equilibrium. Most important of these will be the gradual attainment of an uneven-aged condition through the death of individual trees by accident and disease. The resultant opening of the forest canopy will create conditions significantly different from those previously existing. There will be a marked increase in the numbers of actively-growing sugar maples. Beech will, on the other hand, materially decrease in importance, especially as regeneration by root suckers is insignificant in overmature trees. Hemlock seedlings are never as numerous as those of sugar maple, and this tree will decrease in abundance. The more or less intolerant trees—those which were uncommon in the previous generation—will now have a definite chance to reestablish themselves in windfalls and small openings. Yellow birch will probably be very aggressive, particularly because of its

light wind-borne seeds. The invasion of other intolerants may be locally important. In this connection, observations made in old forests where single trees have been removed show that many intolerant old field species, like *Spiraea latifolia* and *Betula populifolia*, may invade and become temporary components of virgin stands. The relative proportions of the predominant trees in the virgin forest of Colebrook (Nichols 1913b) were estimated as follows: hemlock and beech, about equally abundant, 55 percent, sugar maple 12 percent, yellow birch 10 percent, red oak 6 percent, chestnut 6 percent, white ash and basswood 7 percent, black cherry, black birch, red maple, and white pine 4 percent. These figures would compare favorably with those implied from the trends outlined above.

Even in the absence of all anthropic disturbances for long periods of time, it cannot be assumed that the upland vegetation of the Blandford area would ever become a forest community homogeneous and constant in its floristics and structure. Droughts, floods, freezing rains, severe windfalls, occasional fires, fungous epidemics, insect infestations, cyclical changes in the numbers of grazing, browsing, and bark-eating animals, although catastrophic, are normal events in the life history of the forest. Their intensity and frequency are at present unknown due to the masking effects of the relatively more important factors of lumbering and grazing. Such natural catastrophes as named above would result in floristic and structural variations of the forest more or less different from, and evolving more or less rapidly toward, an ultimate forest type more or less widely distributed. Marked variations in virgin forest have been recorded by Nichols (1913b:211) for the Colebrook forest, and by other investigators working in Arkansas, Pennsylvania, New York, Quebec, and Ontario.

ZONE D ON THE PLATEAU: THE SAVOY AREA

The vegetation types of the general uplands, occurring at the higher elevations of the Plateau, may be classified in the same manner as the types of the Blandford area. The communities of the two regions are in general comparable, with differences in the Abundance and Presence of certain species. Anthropogenic grasslands cover about 5 percent of the total Area and another 10 percent consists of pastures with varying amounts of brush of numerous species. In general, both the climate and the topography are less favorable for agriculture than at lower elevations, and this is reflected in the greater abundance of forests. These are of two types, one unimportant areally, dominated by red spruce, and occurring on abandoned agricultural lands, the other mainly deciduous, composed of the so-called northern hardwoods. This latter is the regional type as it exists today under the influence of man. The woody vegetation of the Savoy uplands is here considered as comprising four communities: the tree and shrub complex of old fields, and the herb strata, shrub strata, and tree strata of the regional forest. These will be discussed in the order named.

THE SAVOY TREE AND SHRUB COMMUNITY OF OLD FIELDS

GENERAL CHARACTERISTICS

This community differs from that of the Blandford area in several significant details. Gray birch is a much less important species, while red spruce is abundant, occupying much the same position as does white pine at lower altitudes. The pine itself is sociologically insignificant. The complete change from pine pastures to spruce pastures, noticed as one is traveling through the Plateau, is the best single index distinguishing the two Areas. The only other floristic difference of importance is the occurrence of *Vaccinium canadense*, and *Abies balsamea*, species practically absent in the Blandford region. The alder is abundant in pastures, pure stands occasionally covering an acre. In such cases a closed mass of vegetation is developed, 10 to 12 feet high, below which is a cover of grasses and rank herbs very similar to that which develops below aspen, gray birch, and sumach. In general, fire cherry and trembling aspen are more common than in the Blandford community, whereas shrub thickets are a less conspicuous feature of the landscape. To what extent the climate may be effective in causing these differences is not evident, since different usage of the fields may be a contributory factor.

THE RED SPRUCE COMMUNITY

The gradual abandonment of pasture land, with selective grazing unfavorable to deciduous species, is responsible for the present abundance of spruce. In the case of immediate and complete abandonment, on the other hand, many deciduous shrubs and trees occupy positions of greatest importance.

Stands of red spruce are usually from 1 to 5 acres in extent, or the community occurs as an irregular belt between forest and agricultural lands. Its abundance on the lower slopes near farms and settlements has often given rise to the strictly local designation of "spruce lowlands" for such sites, as contrasted to the "hardwood slopes" above them. Such a segregation of forest areas is induced by human activities and is not dependent on site conditions, other than those factors such as slope and stoniness, which originally determined the use of the land for agriculture.

Spruce stands are found in all stages of development, from colonies of seedlings in old fields to those where the trees are large enough to be considered mature from the standpoint of the lumber. All such stands are characteristically dense; the interiors are deeply shaded and may be devoid of all lesser vegetation. A large number of species of the forest herb layer eventually appear, but no floristic differences have been noted which would characterize this variant. Shrubs usually play a minor role in the vegetation. In the older stands, seedlings of all the common forest trees have been observed. Nevertheless an estimate of the composition of the naturally succeeding forest is hazardous, because these stands are consistently cut before overmaturing

TABLE 7. Presence and Coverage-when-present of the species of the Savoy Tree and Shrub Community of Old Fields. Figures for Presence refer to stands of 5 acres (2 hectares); those for Coverage-when-present refer to stands of $\frac{1}{4}$ acre (10 ares).

	Coverage			
	100-66 Percent	66-33 Percent	33-1 Percent	1-0 Percent
Presence of 90 percent:				
<i>Picea rubra</i>	50	50	+	
<i>Spiraea latifolia</i>	20	40	40	
<i>Spiraea tomentosa</i>	20	40	40	
<i>Alnus incana</i>	5	15	80	
<i>Rhus typhina</i>	5	15	80	
<i>Acer rubrum</i>	+	10	90	
<i>Populus tremuloides</i>	+	10	90	
<i>Prunus pennsylvanica</i>	+	10	90	
<i>Abies balsamea</i>			100	
<i>Acer saccharum</i>			100	
<i>Betula alba</i> var. <i>papyrifera</i>			100	
<i>Vaccinium pennsylvanicum</i>			100	
Presence of 70 percent:				
<i>Betula populifolia</i>	10	50	40	
<i>Amelanchier canadensis</i>			100	
<i>Prunus virginiana</i>			100	
<i>Rubus allegheniensis</i>			100	
<i>Rubus hispidus</i>			100	
<i>Salix cordata</i>			100	
<i>Salix discolor</i>			100	
<i>Salix rostrata</i>			100	
<i>Vaccinium canadense</i>			100	
<i>Vaccinium corymbosum</i>			100	
<i>Pyrus americana</i>				100
Presence of 50 percent:				
<i>Larix laricina</i>	25	50	25	
<i>Potentilla fruticosa</i>		+	100	
<i>Rubus idaeus</i> var. <i>aculeatissimus</i>		+	100	
<i>Dierilla lonicera</i>			100	
<i>Gaylussacia baccata</i>			100	
<i>Ilex verticillata</i>			100	
<i>Pyrus malus</i>			100	
<i>Pyrus melanocarpa</i>			100	
<i>Viburnum cassinoides</i>			100	
<i>Cornus alternifolia</i>				100
Presence of 30 percent:				
<i>Tsuga canadensis</i>		10	90	
<i>Fagus grandifolia</i>		10	90	
<i>Pinus strobus</i>		+	100	
<i>Betula lutea</i>			100	
<i>Corylus rostrata</i>			100	
<i>Kalmia angustifolia</i>			100	
<i>Lyonia ligustrina</i>			100	
<i>Fraxinus americana</i>				100
<i>Juniperus communis</i> var. <i>depressa</i>				100
<i>Lonicera caerulea</i> var. <i>villosa</i>				100
<i>Nemophanthus mucronata</i>				100
<i>Rhododendron canadense</i>				100
<i>Salix humilis</i>				100
<i>Sambucus racemosa</i>				100
<i>Viburnum dentatum</i>				100
Presence of 10 percent:				
<i>Crataegus</i> spp.				100
<i>Populus grandidentata</i>				100
<i>Rubus odoratus</i>				100
<i>Sambucus canadensis</i>				100
<i>Viburnum opulus</i> var. <i>americanum</i>				100

and the development of advance reproduction. It is inevitable that a mixture of the most tolerant species of the Area, namely beech, sugar maple, hemlock, and spruce, would succeed, with a certain proportion of yellow birch, red maple, ash, and paper birch in the spaces left by windthrown spruce. The forest in every case would be some aspect of the regional Beech-Red Spruce Community.

ASSOCIATED HERB LAYERS

The herbaceous stratum existing under the canopies of certain trees and shrubs, namely gray birch, aspen, tamarack, fire cherry, sumach, and alder—in both Blandford and Savoy areas—is a dense vegetation dominated by grasses. These communities, entirely distinct floristically from the herb layers of the forests, are closely related to those of tilled fields, meadows, and pastures. The grassland under sumach appears to be in temporary equilibrium with the long-lived sumach phase; otherwise these communities are temporary, and are being rapidly invaded by various trees and shrubs of the old-field community. In general, the most conspicuous and characteristic plants of these subarbooreal grasslands are the following:

<i>Dicksonia punctilobula</i>	<i>Lysimachia quadrifolia</i>
<i>Onoclea sensibilis</i>	<i>Apocynum androsaemifolium</i>
<i>Pteris aquilina</i>	<i>Pedicularis canadensis</i>
<i>Botrychium virginianum</i>	<i>Veronica officinalis</i>
<i>Lycopodium clavatum</i>	<i>Antennaria neglecta</i>
<i>Lycopodium complanatum</i>	<i>Aster divaricatus</i>
<i>Lycopodium obscurum</i>	<i>Aster macrophyllus</i>
<i>Agropyron repens</i>	<i>Aster umbellatus</i>
<i>Phleum pratense</i>	<i>Gnaphalium decurrens</i>
<i>Lilium canadense</i>	<i>Gnaphalium polycephalum</i>
<i>Lilium philadelphicum</i>	<i>Hieracium aurantiacum</i>
<i>Thalictrum dioicum</i>	<i>Hieracium canadense</i>
<i>Agrimonia gryposepala</i>	<i>Prenanthes trifoliolata</i>
<i>Potentilla canadensis</i>	<i>Solidago bicolor</i>
<i>Fragaria virginiana</i>	<i>Solidago caesia</i>
<i>Rubus hispidus</i>	<i>Solidago graminifolia</i>
<i>Amphicarpa monoica</i>	<i>Solidago rugosa</i>

THE SAVOY FOREST HERB COMMUNITY

In the herb stratum of the forests, a community occurs which is clearly segregated from the rest of the vegetation, and corresponds closely to that of the Blandford area. The floristic composition is essentially the same, although the various species are distributed differently. Three herbs are so abundant that they more or less characterize the vegetation: *Aspidium spinulosum*, *Lycopodium lucidulum*, and *Oxalis acetosella*. Some species are more rare here; and a few of the southern herbs are entirely absent. Several northern species are more numerous; *Linnaca borealis* here first becomes

constant. The communities of *Polypodium vulgare* on large rocks and boulders in the forest occur in the same abundance as at lower altitudes.

An herb layer is distinctly developed in about 90 percent of the Savoy forests, but is usually absent from dense young stands of beech, sugar maple, hemlock, and red spruce and in situations where yew and hobblebush predominate. This stratum possesses an average Coverage of 50 percent and a maximum of 75 percent. The manner of occurrence of the species is expressed by the data in Table 8.

TABLE 8. Presence and Coverage-when-present of the species of the Savoy Forest Herb Community. Figures for Presence refer to stands of 5 acres (2 hectares); those for Coverage-when-present refer to stands of one acre (100 square meters).

	Coverage			
	100-66 Percent	66-33 Percent	33-1 Percent	1-0 Percent
<i>Aspidium spinulosum</i>	10	40	50	
<i>Lycopodium lucidulum</i>	10	40	50	
<i>Oxalis acetosella</i>	10	40	50	
<i>Picea rubra</i>	10	15	75	
<i>Acer saccharum</i>	+	25	75	
Presence of 70 percent:				
<i>Fagus grandifolia</i>	20	50	30	
<i>Abies balsamea</i>	10	15	75	
<i>Aralia nudicaulis</i>	+	75	25	
<i>Aster acuminatus</i>	+	75	25	
<i>Aster divaricatus</i>	+	75	25	
<i>Aspidium noveboracense</i>		50	50	
<i>Eupatorium urticacifolium</i>		50	50	
<i>Brachyelytrum erectum</i>		25	75	
<i>Clintonia borealis</i>		25	75	
<i>Medeola virginiana</i>		25	75	
<i>Oakesia sessilifolia</i>		25	75	
<i>Polystichum acrostichoides</i>		20	80	
<i>Maianthemum canadense</i>		10	90	
<i>Mitchella repens</i>		10	90	
<i>Polygonatum biflorum</i>		10	90	
<i>Smilacina racemosa</i>		10	90	
<i>Tiarella cordifolia</i>		10	90	
<i>Cornus canadensis</i>		+	100	
<i>Trientalis americana</i>		+	100	
<i>Coptis trifolia</i>			100	
<i>Gaultheria procumbens</i>			100	
<i>Phegopteris polypodioides</i>			100	
<i>Acer rubrum</i>				100
<i>Betula lutea</i>				100
<i>Fraxinus americana</i>				100
Presence of 50 percent:				
<i>Polypodium vulgare</i>	75	25	+	
<i>Osmunda cinnamomea</i>	10	80	10	
<i>Osmunda claytoniana</i>	10	80	10	
<i>Tsuga canadensis</i>	10	50	40	
<i>Epifagus virginiana</i>		+	100	
<i>Collinsonia canadensis</i>		+	100	
<i>Pyrola elliptica</i>		+	100	
<i>Geum canadense</i>			100	
<i>Hydrocotyle americana</i>			100	
<i>Lycopodium clavatum</i>			100	
<i>Lycopodium complanatum</i>			100	
<i>Lycopodium obscurum</i>			100	

	Coverage			
	100-66 Percent	66-33 Percent	33-1 Percent	1-0 Percent
<i>Viola</i> spp.			100	
<i>Actaea alba</i>				100
<i>Actaea rubra</i>				100
<i>Epipactis pubescens</i>				100
Presence of 30 percent:				
<i>Dicksonia punctilobula</i>	50	50	+	
<i>Onoclea sensibilis</i>		50	50	
<i>Asplenium filix-femina</i>		25	75	
<i>Laportea canadensis</i>		10	90	
<i>Amphicarpa monoica</i>		+	100	
<i>Circaea alpina</i>		+	100	
<i>Lycopodium annotinum</i>		+	100	
<i>Phegopteris polypodioides</i>		+	100	
<i>Pyrola americana</i>		+	100	
<i>Pilea pumila</i>		+	100	
<i>Veronica officinalis</i>		+	100	
<i>Arisaema triphyllum</i>			100	
<i>Chiogenes hispidula</i>			100	
<i>Monotropa uniflora</i>			100	
<i>Solidago caesia</i>			100	
<i>Botrychium virginianum</i>				100
<i>Hepatica triloba</i>				100
<i>Prenanthes trifoliolata</i> (?)				100
<i>Streptopus amplexifolius</i>				100
<i>Streptopus roscus</i>				100
<i>Trillium erectum</i>				100
<i>Trillium undulatum</i>				100
Presence of 10 percent:				
<i>Pteris aquilina</i>	25	75		
<i>Impatiens biflora</i>	10	80	10	
<i>Osmunda regalis</i>		50	50	
<i>Asplenium acrostichoides</i>		10	90	
<i>Chimaphila umbellata</i>		+	100	
<i>Equisetum arvense</i>		+	100	
<i>Solidago latifolia</i>		+	100	
<i>Thalictrum dioicum</i>		+	100	
<i>Veratrum viride</i>		+	100	
<i>Corallorhiza maculata</i>			100	
<i>Corydalis sempervirens</i>			100	
<i>Epigaea repens</i>			100	
<i>Aralia racemosa</i>				100
<i>Aspidium cristatum</i>				100
<i>Aspidium marginale</i>				100
<i>Cypripedium acaule</i>				100
<i>Monotropa hypopitys</i>				100

THE SAVOY NORTHERN SHRUB COMMUNITY

The forest shrubs of the Savoy area comprise a single integrated association, the regional counterpart of the Blandford Northern Shrub Community, from which it differs mainly in the extent of local distribution. It is found on about 75 percent of the forest lands, although well developed only on half this amount. The northern shrubs are often absent from young growth and in stands silviculturally treated, while the community occurs most abundantly on lower slopes and in ravines, in which sites yew may be very common. Under natural conditions it would occur in all habitats except possibly the

driest upper slopes. Although floristically similar to the Blandford community, differences in the relative abundance of the species is apparent by a comparison of data in Tables 5 and 9. Optimum development of the community under a uniform upper canopy occasionally occurs, as well as local domination of the site by striped and mountain maples.

Witch hazel is rare; so also is the mountain laurel. The latter thrives on the shores of small lakes, namely, Finerty Pond in Washington, North Pond in Florida, and South Pond in Savoy. Aside from the communities at these stations, the Witch Hazel-Mountain Laurel Community is not represented in this Area.

TABLE 9. Presence and Coverage-when-present of the species of the Savoy Northern Shrub Community. Figures for Presence refer to stands of 5 acres (2 hectares); those for Coverage-when-present refer to stands of $\frac{1}{4}$ acre (1,000 square meters).

	Coverage			
	100-66 Percent	66-33 Percent	33-1 Percent	1-0 Percent
Present of 90 percent:				
<i>Viburnum alnifolium</i>	50	50	+	
<i>Acer pennsylvanicum</i>	50	50	+	
<i>Acer spicatum</i>	50	50	+	
Presence of 70 percent:				
<i>Taxus canadensis</i>	50	50	+	
<i>Cornus alternifolia</i>			+	100
<i>Lonicera canadensis</i>			+	100
Presence of 50 percent:				
<i>Corylus rostrata</i>				100
Presence of 30 percent:				
<i>Sambucus racemosa</i>				100

THE SAVOY BEECH-RED SPRUCE COMMUNITY

The important position occupied by the Beech-Hemlock Community in the Blandford area is comparable to that assumed by the Beech-Red Spruce Community in the Savoy area. Red spruce has not ecologically replaced hemlock but has been added to the community, while hemlock has become less common. Red oak, white pine, basswood, black birch, and hop hornbeam are either absent or of no significance in the forest. On the other hand, sugar maple, yellow birch, red maple, white ash, black cherry, and paper birch hold about the same positions as they do in the Blandford area, although the last-named is often more common. All these species are very similar to each other in their ecological requirements in the forest, and there seem to be no valid grounds for recognizing more than a single community for the forests here discussed.

Reproduction of the various forest trees is essentially similar to that at lower altitudes, although young red spruce trees often preempt much of the available space, and balsam fir seedlings are locally common. This last-named species is only rarely found in the upper canopy, and, because of its high mortality at all ages, does not seem destined to assume any greater importance in the future. The status of balsam fir is apparently comparable to its position in northern Cape Breton Island, in that its inability to assume a

TABLE 10. Presence and Coverage-when-present of the species of the Savoy Beech-Red Spruce Community. Figures for Presence refer to stands of 5 acres (2 hectares); those for Coverage-when-present refer to stands of 2½ acres (1 hectare).

	Coverage			
	100-66 Percent	66-33 Percent	33-1 Percent	1-0 Percent
Presence of 90 percent:				
<i>Fagus grandifolia</i>	25	50	25	
<i>Acer saccharum</i>	10	45	45	
<i>Betula lutea</i>	10	45	45	
<i>Fraxinus americana</i>	10	45	45	
<i>Acer rubrum</i>		25	75	
<i>Picea rubra</i>	—	10	90	
<i>Betula alba</i> var. <i>papyrifera</i>		10	90	
Presence of 70 percent:				
<i>Tsuga canadensis</i>	10	45	45	
<i>Prunus serotina</i>			—	100
Presence of 50 percent:				
<i>Abies balsamea</i>				100
Presence of 10 percent:				
<i>Betula lenta</i>				100

dominant position in the forest is due to "its shorter tenure of life, coupled with its greater susceptibility to fungous diseases and its less pronounced tolerance of shade" (Nichols 1918:290). With the third of these factors, the author would draw exception for the Plateau, for balsam fir is repeatedly found in such situations as would indicate a tolerance approaching, or equal to, that of the three species named above. Although such a statement may first appear to be at variance with Cooper's (1913) to the effect that "later in life the young trees [balsam fir, on Isle Royale, Lake Superior] can endure severe shading, but for a successful start abundant light seems to be a necessity," it must be remembered that, apart from a difference in climatic conditions which may be less favorable to balsam, the Isle Royale forests are a mosaic of windfall areas succeeding each other on short rotation, and conditions on the site alternate between extremes of shade and exposure. In the Savoy forests, balsam fir is not dominant, mainly because of severe competition with associated species. That the climate of this part of the Plateau is highly favorable, however, is shown by its abundance and good development in abandoned pastures.

No segregate comparable to the Blandford Summit Community exists in the Savoy area. The shrubby type of growth typically occurs on hill tops; but red spruce may tend to dominate such sites by reason of its more pronounced vertical growth. The leader in all cases remains erect and the lateral branches are restricted to the lee side, producing the well-known flag form. On one of the highest and most exposed summits atop the Hoosac Range the vegetation, though mutilated by fire, shows a floristic composition in regard to trees and shrubs identical to that of the general upland forests. The only exception is in the local frequency of *Claytonia virginiana*, *Erythronium americanum*, and *Trillium erectum*.

Anthropic activities, although not changing the identity of this community, have altered its composition and appearance over large areas in a most striking way. Red spruce is the most valued of the trees, and with the introduction of the portable sawmill, small isolated groups have been removed from the forest. Hemlock in distribution is quite irregular, being common in some places and relatively rare in others, a condition due in part but not entirely to the adverse effects of clear-cutting. Both evergreen trees consequently are largely absent from the forest, and deciduous stands of northern hardwoods are predominant. Spruce seedlings, which are very tolerant of shade, are again appearing in the reproduction, and with the increasing attention paid to silvicultural practices, the species is destined to become much more important. At the present time the forest is mainly deciduous, in striking contrast with the abandoned spruce-covered pastures.

Existing vegetation has been interpreted elsewhere in the United States in terms of actively migrating types and changing climate. A hasty survey of the Savoy area might lead one to believe that the northern coniferous forest, represented by red spruce and fir, is migrating southward into an area of northern hardwoods and that this migration is being facilitated by the existence of abandoned pastures which are open to invasion. Such an interpretation is superficial and illogical, and ignores the fact that with a given flora and climate, historic influences and anthropic activities may induce communities greatly differing in dominants, physiognomy, and structure, without any change in the general environment of the area.

Although no tract of virgin timber has been located in the Savoy area which might serve to indicate the nature of the original vegetation, the future development of existing stands is predictable. Red spruce and beech in mixture, with or without hemlock, would eventually form more than half the bulk of the forest growth. The first is susceptible to windfall, and because of the resulting openings in the forest canopy, there would be a fairly high proportion of such species as sugar maple, ash, and yellow birch, species which require at least a partial opening to become established in the upper canopy. Other tree species would hold very minor positions. As at lower elevations, the ultimate vegetation would be in dynamic equilibrium, with variations in flora, structure, and physiognomy due to catastrophes natural in the life history of the forest.

SUMMARY

The study here reported upon concerns the upland vegetation of the Berkshire plateau of western Massachusetts. The underlying rocks, the glacial topography, and the various soil series in this region are not correlated with the more important types of vegetation. Biotic factors, particularly the decrease in grazing and gradual abandonment of pastures in recent times, have determined significant variations in the existing vegetation.

The shrubs and trees of this region are derived from two floristic centers, one the region of the Great Lakes and the St. Lawrence valley, the other the southern Appalachians and the Ohio River valley. Each of these floristic centers possesses both evergreen and winter-deciduous gymnosperm and angiosperm trees, and many shrubby and herbaceous species; they are not to be confused with centers of vegetation types.

The vegetation communities recognized in this paper are those which stand out as most clearly distinct in the complex of natural vegetation, and which are of most practical value in the attempt at an orderly description of facts and phenomena which, in themselves, do not exist in complete orderliness. In every case these units have been determined independently, with reference to the facts actually observed on the ground and not, as far as humanly possible, on the basis of predetermined ideas or rigidly defined principles. In no case are these units to be identified with those of *a priori* systems in current usage. Life form, growth form, and dominance are not recognized as classificatory characters of primary importance.

Bray's vegetation zones of New York State are extended to western New England, where three of these are found on the Plateau.

"Zone B," characterized by chestnut, oaks, hickories, and tulip poplar, and dominantly austral in flora and vegetation, occupies the lower elevations.

"Zone C" with sugar maple, beech, yellow birch, hemlock, and white pine occurs at intermediate elevations. The old fields here are characterized by gray birch, white pine, and about 50 secondary species. These species, presumably intolerant, are frequently found on poorly drained mineral soils, lake shores, stream banks, trail sides, hill tops, and other situations where competition with the regional forest species is less severe and where they can emerge into dominance. Isolated islands of oak and hickory are found on some of the exposed summits. The regional forest herb community is characterized by about 100 species, mainly boreal. Mountain laurel and witch hazel are the most abundant forest shrubs; striped maple, mountain maple, hobblebush, and yew are also common. The existing regional forest which is destined to continue essentially unchanged in composition, is predominantly beech and hemlock, with sugar maple and yellow birch abundant, also white ash, red oak, red maple, basswood, black cherry, and paper birch.

"Zone D" with the dominant trees of Zone C, plus red spruce, balsam fir, and paper birch occurs at highest altitudes. Red spruce is most abundant in old fields, with less gray birch than in Zone C and no white pine. The forest herbs are similar to those of the preceding zone, with *Aspidium spinulosum*, *Lycopodium lucidulum*, and *Oxalis acetosella* predominant. Mountain laurel and witch hazel are rare; typically northern forest shrubs are abundant. The regional forest is dominantly beech and red spruce; red oak, white pine, and basswood are very rare; sugar maple, yellow birch, hemlock, red maple, white ash, black cherry, balsam fir, and paper birch are common.

The zonation of western Massachusetts vegetation serves as a classification of value to pure science and of immediate application to such applied sciences as forestry, agriculture, soil conservation, and watershed management. The method places minor emphasis on such conspicuous but at times secondary affinities as similarities in life form, growth form, leaf form, consociational cover types, dominance, and community structure; whereas it strongly emphasizes the fundamental homogeneity of flora and climate, and the potentialities of the sites for bearing types other than those now in existence.

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AN ECOLOGICAL TRANSECT OF BLACK MOUNTAIN,
KENTUCKY

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AN ECOLOGICAL TRANSECT OF BLACK MOUNTAIN, KENTUCKY¹

INTRODUCTION

Black Mountain, clothed throughout with mixed deciduous forest, is situated in southeastern Kentucky, and for many miles the Kentucky-Virginia boundary follows its crest. It occupies a central position in the Cumberland Mountains, that is, Cumberland Mountains physiographic section (Fenneman, 1938), with Pine Mountain flanking it on the west, and Cumberland Mountain and Stone Mountain on the east. In general the crest of Black Mountain trends northeast-southwest, but actually it is a very crenulous line some forty miles in length. Its slopes are cut by numerous small streams with steep gradients; those on the Kentucky side are tributary to Poor Fork or Clover Fork of the Cumberland River. Between these streams are ridges and spurs whose slopes at first descend gradually from the mountain summit, then steeply, with an average fall of one foot in two. Mountain slopes of 45° are frequent on the sides of these ridges—the slopes from spur to stream.

The summit of Black Mountain ranges generally between 3,000 and 4,000 feet in elevation, reaching 4,250 feet at its highest point, the Doubles, in Harlan County. The valley of Poor Fork of the Cumberland River, at its west base, falls from 1,700 feet at the head of the valley to 1,100 feet at the junction of Poor Fork and Clover Fork near Harlan.

Geologically, Black Mountain occupies a central position in a syncline, hence its strata are essentially horizontal. It has been carved from a Tertiary peneplain by subsequent erosion, and owes its elevation to the superior hardness of certain sandstones. From base to summit, the underlying rocks belong to the Pennsylvanian series (Coal Measures), including, hence, alternating shales, coal seams, and sandstones. However, bed-rock is exposed in but few places (except in stream beds) and the mountain slopes generally are covered by a deep soil mantle. The influence of underlying rock on the character of the soil is seldom discernible, except on narrow ridges and convex west-to-south slopes. Soils are for the most part mature. These features are in strong contrast to those of nearby Pine Mountain where the character of underlying rock so strikingly influences vegetation (Braun, 1935).

The vegetation of Black Mountain reflects, then, the vegetational response to the climatic conditions of the region, modified only by variations in soil moisture and evaporating power of the air brought about by slope exposure. Developmental communities (except those of secondary vegetation) are lacking or occupy so little space as to be negligible. Everywhere the vegetation

¹ This is the second of a series of papers on the forests of eastern Kentucky. Some will be detailed treatments of local areas which emphasize the relations between communities and environment, and give data on which present and future interpretations may be based; others will deal in a more general way with broader regions.

seems to have reached stability, to be climax in nature. Yet it is not uniform throughout. Forest composition varies with slope exposure, and also, varies altitudinally, from valley to mountain summit. The whole is a mosaic of segregates of the mixed mesophytic forest association. The slope or topographic situation occupied by each association-segregate² in a region where a number of such segregates occur side by side suggests their genetic relationships and aids in the interpretation of the inter-relations and climatic dependencies of the major associations of the deciduous forest formation.

To the National Research Council, grateful acknowledgment is made of a grant for aid in studies in the field season of 1935, during which time a part of the observations for this paper were made. To the writer's sister, who has been a companion throughout all of the field studies, thanks are extended.

RECORD OF OBSERVATIONS

The present paper presents the results of a detailed study of forest composition in a limited area on Black Mountain (Fig. 1). The location was selected after three field seasons of study in the Cumberland Mountains in Letcher and Harlan counties, because the communities encountered in this area are fairly representative of the variations found on Black Mountain as a whole, and because it was possible here to follow sequences, unbroken by serious interruption, from valleys to mountain summit.

The observations were made along nine transects (totaling about nine miles in length) differing from one another in contour and slope exposure, and at additional sites affording conditions not adequately represented along the transects. The transects are not belts of uniform width but vary to some extent laterally. That is, while definite lines were followed (as indicated on the map) studies were extended to either side as variations in topography demanded. Locations were selected to emphasize contrasts due to slope exposure. The area of the map is divided by the nearly east-west crest of River Ridge. On one side of River Ridge, the northwesterly slopes of the mountain descend to the Cumberland Valley; on the other side are southerly slopes to the Left Fork of Colliers Creek.

The accompanying map (Fig. 1), enlarged and adapted from the Whitesburg topographic sheet, shows the general features of the topography of the area, and the location of transects and of places mentioned in the text. In Figure 2 are shown profiles of five transects.

Studies on the northwesterly slope of the mountain, the slope toward the Cumberland Valley, include much of the valleys and ridges of Joe Day Branch, Meeting House Branch, and Staggerweed Hollow. Southerly slope studies were made in the valley of the Left Fork of Colliers Creek where two transects traverse the slopes of River Ridge from creek to summit, and in the upper Left Fork of Colliers Creek.

² For definition of association-segregate, see Braun, 1935a.

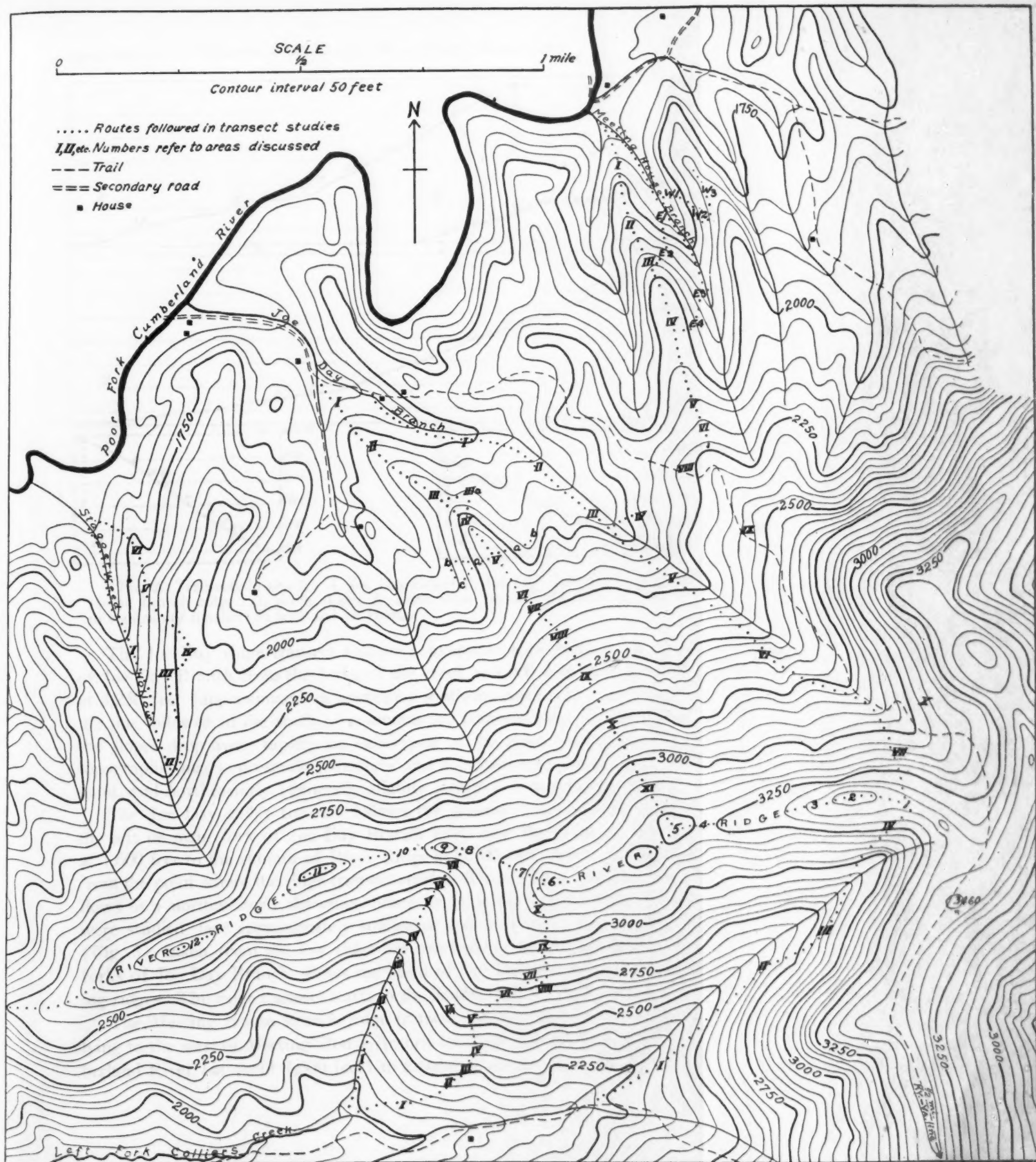


FIG. 1. Topographic map of area studied (adapted from Whitesburg topographic sheet), showing location of transects and of communities shown on charts.



FIG. 1. Topographic map of area studied (adapted from Whitham, 1964), showing location of transects and of community zone.

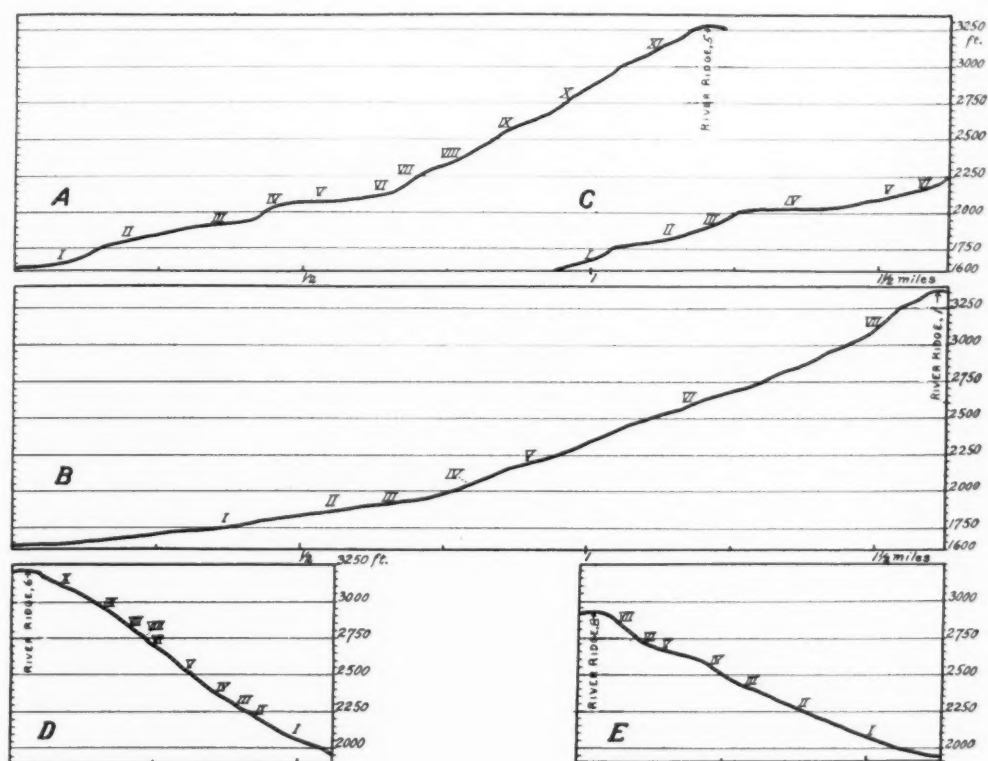


FIG. 2. Transects in profile: A, Joe Day ridge; B, Joe Day Branch; C, Meeting House Branch ridge; D, south slope; E, south slope ravine. Numbers correspond to community numbers in text and on charts.

The Joe Day ridge transect follows a mountain spur between the forks of Joe Day Branch from the forks of the creek at 1,600 feet to River Ridge at 3,250 feet (approximately a northwest-southeast line) where it intercepts the line followed in the study of mountain top communities. In many places the slopes drop away rapidly on either side of the ridge (not evident from topographic map), presenting westerly and southwesterly slopes on the one hand, and northeasterly (generally slightly steeper) slopes on the other.

The Joe Day valley transect follows the general course of the valley of the left or main fork of Joe Day Branch from near the forks of the creek at 1,600 feet to the summit of River Ridge at 3,400 feet, about one-half mile from the point where the ridge transect reaches River Ridge. Joe Day Branch flows in a northwesterly direction, hence its opposing slopes, both of which were studied, face approximately southwest and northeast. The photograph (Fig. 3), taken from the low ridge-top overlooking and to the west of the forks of Joe Day Branch, shows the basin of Joe Day Branch and its limiting ridges. The ridge transect starts in the hemlocks at the forks of the creek.

The Meeting House Branch ridge transect follows the crest of the ridge lying to the west of Meeting House Branch from the flat bordering the Cumberland River (at about 1,600 feet) to a point at about 2,250 feet where this

ridge overlooks the valley of Joe Day Branch. This ridge trends in an almost north-south direction, sloping north, hence introduces conditions not met on the Joe Day ridge.



FIG. 3. General view of the basin of Joe Day Branch. The ridge transect starts in the hemlocks (darker trees) in the lower left-hand corner, reaching the crest of River Ridge at the high knob on skyline at right. The valley transect follows up the main valley to the left of this ridge. Range of elevation, 1,600 to 3,400 feet. July.

The southerly slope transect follows in general a convexity of slope on the south face of River Ridge, ascending from 2,000 feet on the Left Fork of Colliers Creek to 3,200 feet on River Ridge where it intercepts the line followed in the study of mountain top communities at a point close to the upper end of the Joe Day ridge transect.

The south slope ravine transect follows a ravine on the southerly slope of River Ridge from the Left Fork of Colliers Creek at 2,000 feet to the crest of River Ridge at about 2,900 feet. Additional studies near the headwaters of the Left Fork of Colliers Creek are included with the south slope ravine. The upper part of the valley of the Left Fork of Colliers Creek and the south slope traversed by the transect are shown in Figure 4.

Mountain top communities were studied along the crest of River Ridge. This is one of the longest spurs of Black Mountain, and extends nearly four miles from the mountain crest on the Kentucky-Virginia line. Its axis varies from east-west to northeast-southwest.



FIG. 4. General view of the head of the valley of the Left Fork of Colliers Creek and (left) the south slope traversed by the transect. Dead chestnut on the crest of River Ridge in foreground. The profile of the slope rising obliquely to the left from the lower right-hand corner is marked by a band of oak-chestnut forest not yet in leaf and is, approximately, the strip traversed by the transect. Below this to left are the round lighter crowns of trees of mixed mesophytic forest, in leaf. The opposite slope of the valley, to the right and above the oblique band, is mixed mesophytic, distinguished at a distance by the roundish spots of tree crowns. On the distant skyline, areas of oak-chestnut forest may be distinguished by the open appearance of trees not yet in leaf. May 8.

The communities encountered along the several transects, ravines, ridge crests and slopes are representative of the general region—the Cumberland Mountains—and in detail display what may be expected on the Kentucky slopes of Black Mountain, and to a considerable extent also, on the slopes of the Log Mountains in Bell County. That is, this small area is representative of Kentucky southeast of Pine Mountain.

Detailed records of observations are included in this paper, for it is upon such observations that generalizations are based and from which interpretations are made. In view of the unstable state and changing viewpoints of human interpretations, and because of the rapidly diminishing amount of primeval deciduous forest available for study, records may be of value in future interpretations. While the data recorded here were obtained from studies within the four square miles covered by the map, the interpretations of communities are made in the light of these and other observations in many places in both Letcher and Harlan counties. The broader features will be considered in a study of the vegetation of the Cumberland Mountains.

Forest composition of communities along the transects is necessarily based on smaller forest areas than would be desirable in a regional study, though in all cases the greatest possible length of area was included. Narrowness of ridge and hence small size of community occasionally necessitates recording communities of few trees. However, the recognition of communities as representatives of definite association-segregates is in all cases based upon their frequent recurrence and large extent in the region as a whole.

Approximate percentages of all *canopy* species of each community are shown in charts (Figs. 5, 7, 10, and 15 to 20). These are based on primary stands not modified by cutting. In all except the more xeric communities, canopy trees generally range from 2½ to 4 feet, or occasionally up to 8 feet, d. b. h.³ Standing dead chestnut was included in the counts on which these percentages are based. The study of inferior layers of the forest is much less detailed, in places very incomplete. Season of observation, also, has had an effect upon the record of herbaceous plants. Lists, therefore, are representative of composition rather than exhaustive.

The location of communities considered in the text is shown on the map (Fig. 1) and on profiles (Fig. 2) by Roman and arabic numerals corresponding to those in the text and on the charts and tables.

COMMUNITIES OF THE NORTHWESTERLY SLOPE

JOE DAY RIDGE TRANSECT

The Joe Day ridge transect traverses the ridge between the forks of Joe Day Branch (Figs. 1 and 2A). The composition of the forest canopy of communities along this transect is shown in Figures 5 and 7. Tables 1 and 2 give lists of understory, shrub and ground layer species.

I. Hemlock dominates the forest of the lowest part of the ridge crest and its lateral slopes, comprising 75 percent of the stand. The extent of this community is apparent in the general view of the area (Fig. 3). The understory is dominantly *Rhododendron maximum*, with *Kalmia latifolia*, *Cornus florida*, *Liriodendron*, *Oxydendrum*, *Amelanchier* and *Tsuga*.

A sparse herbaceous layer including a few distinctive plants reflects the influence of continuous shading by the predominantly evergreen canopy and of the conifer and ericaceous leaf litter (Table 1). The soil profile shows a layer of duff (mor),⁴ beneath which is a brown matted soil a few inches deep overlying a brown sandy mineral soil.

II. Hemlock begins to drop out and chestnut increases, forming about 60 percent of the stand. The transition is fairly abrupt, and is emphasized by the change in aspect due to the different life-form of the dominants of these adjacent and intergrading communities. The understory is more varied than

³ Diameter breast high.

⁴ Duff and mull are used in this paper as defined by Romell and Heiberg (1931); mor is a term which has been used more recently for that type of humus layer which is separated sharply from the mineral soil (Heiberg, 1937, 1939).

AREA No.→ No. of TREES	I	II	III	IIIa	IV	V	VI	VII	VIII	IX	X	XI	EW	TOTAL
	36	64	41	18	23	23	24	21	31	25	38	31	229	375 %
<i>Castanea dentata</i> chestnut														37.6
<i>Quercus montana</i> chestnut oak														31.2
<i>Tsuga canadensis</i> hemlock														8.5
<i>Fagus grandifolia</i> beech														5.6
<i>Quercus coccinea</i> scarlet oak														4.8
<i>Quercus alba</i> white oak														2.7
<i>Acer rubrum</i> red maple														2.1
<i>Carya</i> spp. hickory														1.8
<i>Pinus rigida</i> pitch pine														1.0
<i>Prunus serotina</i> wild black cherry														1.0
<i>Quercus borealis maxima</i> red oak														.8
<i>Acer saccharum</i> sugar maple														.8
<i>Nyssa sylvatica</i> sour gum														.5
<i>Liriodendron tulipifera</i> tulip tree														.3
<i>Betula allegheniensis</i> birch														.3
<i>Magnolia Fraseri</i> mountain magnolia														.3
<i>Oxydendrum arboreum</i> sourwood														.3
<i>Amelanchier canadensis</i> service berry														.3

FIG. 5. Percentage composition of canopy of forest communities along the Joe Day ridge transect. Note differences in percentage of chestnut and chestnut oak in contiguous communities.

in the hemlock forest. In the shrub layer the proportion of *Kalmia* increases; *Rhododendron* decreases. The herbaceous layer continues sparse.

A thin layer (about one inch) of matted root and leaf duff (mor) covers the ground. A leached layer of pale gray sandy soil about one inch deep covers the yellowish sandy soil beneath.

The slopes on either side of the ridge crest differ, the northerly more mesophytic slope with beech-chestnut forest and *Rhododendron* understory; the southwesterly slope (unprotected by opposing ravine slope) (see map) with a xerophytic oak or oak-chestnut forest in which scarlet oak is dominant (see Fig. 7 and Table 2). *Kalmia* replaces *Rhododendron* on the ridge crest and southwest slope (Fig. 8A).

III. Above a projecting point of resistant sandstone the narrow ridge crest is more level. The forest is oak-chestnut with an admixture of mesophytic species. The shrub layer is dominantly *Kalmia* with scattered *Rhododendron*, *Vaccinium*, *Azalea*, and *Smilax* (Fig. 6). The ground layer reflects the siliceous soil and ericad leaf litter.

UNDERSTORY TREES	HERBS										
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
<i>Acer rubrum</i>	X	X									
<i>Acer saccharum</i>	X	X									
<i>Aemiliana canadensis</i>	X	X									
<i>Carya sp.</i>	X	X									
<i>Castanea dentata</i>	X	X									
<i>Cornus florida</i>	X	X									
<i>Fagus grandifolia</i>	X	X									
<i>Fraxinus sp.</i>	X	X									
<i>Liriodendron tulipifera</i>	X	X									
<i>Magnolia acuminata</i>	X	X									
<i>Magnolia fraseri</i>	X	X									
<i>Nyssa sylvatica</i>	X	X									
<i>Ostrya virginiana</i>	X	X									
<i>Oxydendrum arboreum</i>	X	X									
<i>Prunus serotina</i>	X	X									
<i>Quercus alba</i>	X	X									
<i>Quercus borealis maxima</i>	X	X									
<i>Quercus coccinea</i>	X	X									
<i>Quercus montana</i>	X	X									
<i>Tilia heterophylla</i>	X	X									
<i>Tsuga canadensis</i>	X	X									
SHRUBS & WOODY CLIMBERS											
<i>Aristolochia macrophylla</i>											
<i>Hamamelis virginiana</i>											
<i>Kalmia latifolia</i>											
<i>Pyrola puberula</i>											
<i>Rhododendron (Azalea)</i>											
<i>calendulaeae</i>											
<i>Rhododendron (Azalea), Red</i>											
<i>Rhododendron maximum</i>											
<i>Rubus allegheniensis</i>											
<i>Silene spaldingii</i>											
<i>Silene spaldingii</i>											
<i>Vaccinium corymbosum</i>											
<i>Vaccinium stamineum</i>											
<i>Vaccinium vacillans</i>											
<i>Viburnum acerifolium</i>											
<i>Vitis bicolor</i>											
GROUND HERBS											
<i>Chimaphila maculata</i>											
<i>Epigaea repens</i>											
<i>Galax apophylla</i>											
<i>Gaultheria procumbens</i>											
FERNS											
<i>Aspidium marginale</i>											
<i>Aspidium novboracense</i>											
<i>Dicksonia punctilobula</i>											
<i>Polystichum acrostichoides</i>											
<i>Pteris aquilina</i>											

HERBS											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
<i>Aemionella thalictroides</i>											
<i>Antennaria plantaginifolia</i>											
<i>Anemone virginiana</i>											
<i>Ascyrum hypericoides</i>											
<i>Aster divaricatus</i>											
<i>Aureolaria (Garardella) laevigata</i>											
<i>Cimicifuga racemosa</i>											
<i>Claytonia caroliniana</i>											
<i>Conopholis americana</i>											
<i>Coreopsis major</i>											
<i>Cypripedium acaule</i>											
<i>Delphinium tricolor</i>											
<i>Dentaria laciniata</i>											
<i>Dioscorea villosa</i>											
<i>Disporum lanuginosum</i>											
<i>Epipactis pubescens</i>											
<i>Galium lanceolatum</i>											
<i>Geranium maculatum</i>											
<i>Helleborus divaricatus</i>											
<i>Heuchera longiflora</i>											
<i>Hieracium Gronovii</i>											
<i>Hieracium venosum</i>											
<i>Houstonia tenuifolia</i>											
<i>Hypoxis hirsuta</i>											
<i>Lysimachia quadrifolia</i>											
<i>Iris oristata</i>											
<i>Medeola virginiana</i>											
<i>Mitella repens</i>											
<i>Panicum Boscii</i>											
<i>Podocarpus canadensis</i>											
<i>Podophyllum peltatum</i>											
<i>Polygonum verticillatum</i>											
<i>Polygonatum biflorum</i>											
<i>Ranunculus hispidus</i>											
<i>Sanguinaria canadensis</i>											
<i>Sedum ternatum</i>											
<i>Senecio obovatus</i>											
<i>Silene spaldingii</i>											
<i>Solidago sp.</i>											
<i>Thalictrum integrifolium</i>											
<i>Thalictrum dioicum</i>											
<i>Thlaspi aureum atropurpureum</i>											
<i>Tipularia discolor</i>											
<i>Trillium grandiflorum</i>											
<i>Urtica perfoliata</i>											
<i>Urtica grandiflora</i>											
<i>Viola caroliniana</i>											
<i>Viola conspersa</i>											
<i>Viola hastata</i>											
<i>Viola rotundifolia</i>											
<i>Viola sp.</i>											

TABLE 1. Undergrowth of forest communities of Joe Day ridge transect, Fig. 5.

The slopes of the ridge contrast strongly, the northerly slope showing little influence, either in canopy or ground layer, of the sandstone which so strongly affects the vegetation of the drier ridge and westerly slope (Figs. 7, 8B, Table 2). No distinction can be made between the ridge forest and that of the westerly slope for several hundred feet down, except that there are fewer species on the slope. On the northerly slope, the forest is mixed mesophytic,

with chestnut, sugar maple and beech forming approximately 70 percent of the canopy. The humus layer is mull, supporting a rich and varied herbaceous growth.



FIG. 6. Oak-chestnut forest of area *III* of Joe Day Ridge.

Inexplicable variations occur from place to place. Near area *III* is a short spur ridge (Fig. 8C); the axis of the main ridge points northwest, of the spur ridge, area *IIIa*, north. On the main ridge chestnut and chestnut oak share dominance; on the spur ridge chestnut dominates, chestnut oak is a minor constituent and beech is prominent especially in the understory; *Rhododendron* forms a dense heath layer. While there is a difference in the direction of the axes, both are relatively flat-topped areas. That such minor

AREA No.→ No. of TREES	N II SW 17 64 17			N III SW 69 41 32			N IV SW SW SW 26 43 23 58 36 27						N VII 12 21		N X SW 72 38 19		
<i>Castanea dentata</i> chestnut																	
<i>Quercus montana</i> chestnut oak																	
<i>Tsuga canadensis</i> hemlock																	
<i>Fagus grandifolia</i> beech																	
<i>Quercus coccinea</i> scarlet oak																	
<i>Quercus alba</i> white oak																	
<i>Acer rubrum</i> red maple																	
<i>Carya</i> spp. hickory																	
<i>Pinus rigida</i> pitch pine																	
<i>Prunus serotina</i> wild black cherry																	
<i>Quercus borealis maxima</i> red oak																	
<i>Acer saccharum</i> sugar maple																	
<i>Nyssa sylvatica</i> sour gum																	
<i>Liriodendron tulipifera</i> tulip tree																	
<i>Betula allegheniensis</i> birch																	
<i>Oxydendrum arboreum</i> sourwood																	
<i>Amelanchier canadensis</i> service berry																	
<i>Tilia heterophylla</i> + basswood																	
<i>Fraxinus biltmoreana</i> ash																	
<i>Magnolia acuminata</i> cucumber tree																	
<i>Aesculus octandra</i> buckeye																	
<i>Juglans nigra</i> walnut																	

FIG. 7. Comparison of percentage composition of canopy of selected forest communities along Joe Day ridge and the adjacent slope forests. Numbers correspond to those in Fig. 5. Letters refer to direction of slope and location. Emphasizes contrast of slopes.

factor changes may produce pronounced differences indicates clearly the tension between climatic and edaphic factors. From these flat-topped areas (III and IIIa), both main ridge and spur ridge rise steeply to the flat-topped junction of the two in area V. Such sharp rises due to resistant sandstone are generally accompanied by marked increase in chestnut oak. Here, however, chestnut dominates (area IV) and a few pitch pines skirt the edge of the declivity (Fig. 8C, D); *Kalmia* forms dense thickets.

V. A long relatively flat-topped portion of the ridge (area V) appears as a slight saddle discernible in Figure 3. The forest here is chestnut-chestnut oak-beech. The understory is mixed: beech, red maple, white oak, chestnut, tulip tree, red oak, sourwood and hemlock; an open heath layer is made up of *Kalmia*, *Rhododendron*, *Vaccinium vacillans*, *V. corymbosum*, and *Rhododendron* (*Azalea*) *calendulaceum*.

Again the contrast between the slopes of the ridge is pronounced (Fig. 7 and Table 2) but the features are different from those of area III. Over most of the southwest slope adjacent to area V, beech makes up about 50

percent of the canopy, chestnut and chestnut oak together about 30 percent. The understory is mixed and heaths are important in the shrub and ground layers. The aspect of the whole is beech heath (Fig. 9). In the spots opened up by the dying of chestnut, beech, tulip tree, and sugar maple saplings are growing rapidly.

[illegible]

TABLE 2. Undergrowth of forest communities shown in Fig. 7, illustrating contrast of slopes along Joe Day ridge. Lower layers of *II*, *N* and *SW*, and *III*, *SW*, not listed except as seen from ridge.

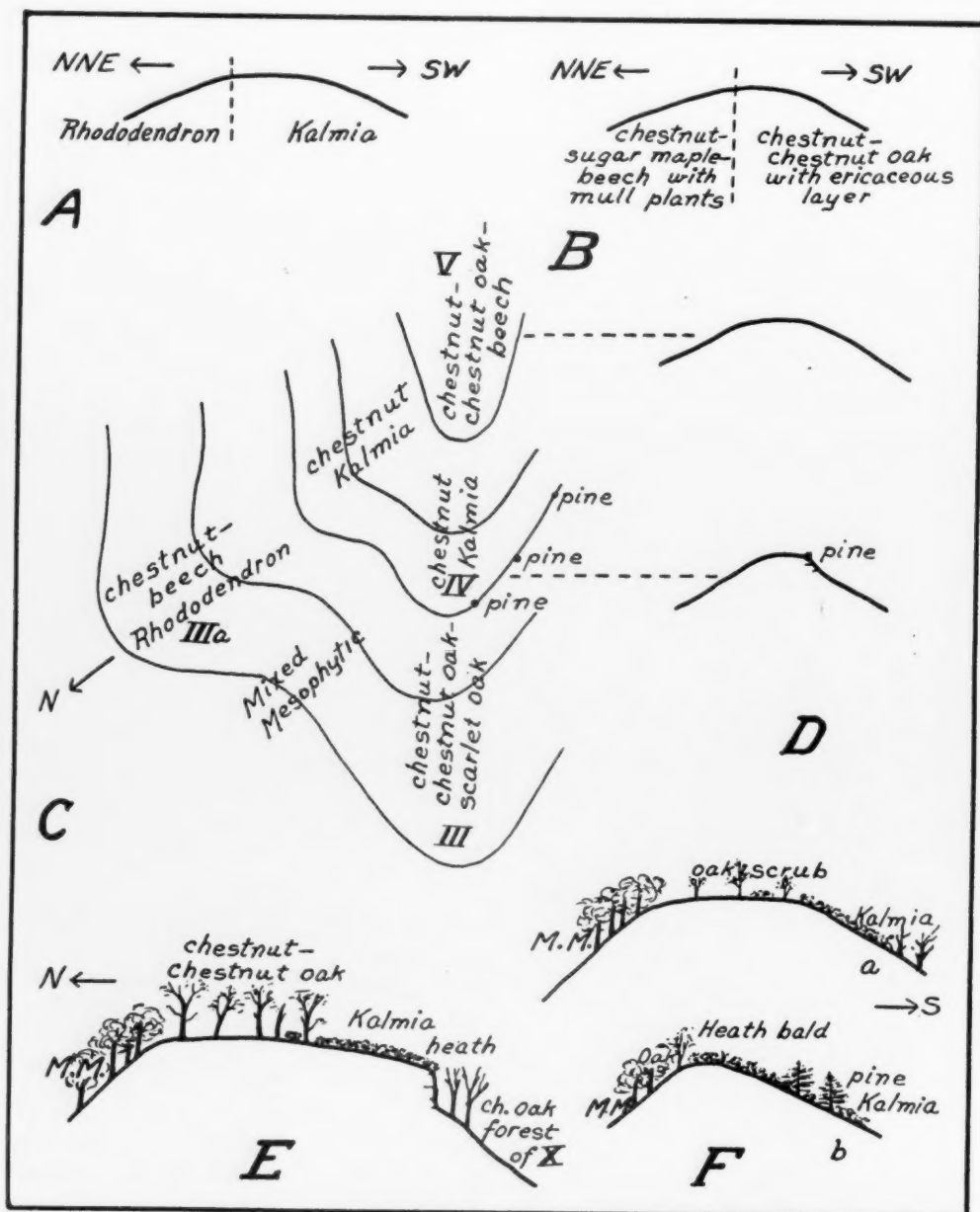


FIG. 8. A, Transverse profile on Joe Day ridge in area II; B, in area III. C, sketch map showing main ridge and spur ridge, areas III, IIIa, IV, V; D, transverse profiles on Joe Day ridge in areas IV and V; E, the upper end of the south slope transect and the crest of River Ridge at 6; F, narrow parts of River Ridge, (a) with oak scrub at 11 and (b) with heath bald at 2. (From field sketches.)

The forest of the other slope (north-northeast) is mixed mesophytic with sugar maple (47 percent), basswood (18 percent) and chestnut (13 percent) most important. A slight change in direction of this slope to north-west (see map, Fig. 1) results in increase in white oak and tulip tree and decrease in basswood (Fig. 7, V, Nb). Beech is not a constituent of these

northerly slope forests, though an important constituent of the forest of the adjacent ridge top and southwesterly slopes.

Higher, above the beech saddle of area *V*, the gradient of the mountain slope is steeper, and the ridge less apparent on the topographic map, appearing only as a convexity of slope. Where this is true, contrasts of slopes are not readily made. In many places, the ridge is still obvious, and sometimes very narrow.



FIG. 9. Beech-chestnut-chestnut oak forest with *Kalmia* and *Rhododendron*; in (a) of southwest slope of area *V*, Joe Day ridge. July.

VI-IX. On these steeper slopes, the forest is the chestnut oak or chestnut oak-chestnut ridge type, with scattered ericads and a poor herbaceous layer. Beech is unimportant. Where the ridge narrows (at *VII*), the number of tree species decreases and *Kalmia* increases; the contrast with the northerly slope, where mixed mesophytic forest prevails, is great (Fig. 7). It should be noted that beech is not a constituent of this forest, but is confined to the ridge. Where the ridge flattens (*VIII*), chestnut increases and beech is more important, although confined to the ridge crest in company with chestnut and chestnut oak. Even on steep rises dominated by chestnut oak, occasional beech trees are found; this is at the upper altitudinal limit of beech. On the steepest slopes, if soil is shallow, chestnut oak forms 90 to 95 percent of the canopy and dominates also in the reproduction (area *IX*).

X. For approximately 1,000 feet in elevation this alternation of chestnut oak-chestnut and chestnut, and of *Kalmia* belts and open undergrowth continues. Wherever the ridge breaks away to steep northerly slopes, mixed mesophytic forest prevails. On the ridge, sugar maple appears in the undergrowth above 3,000 feet, and occasionally in the canopy of less steep parts of the southwest slopes of the ridge (see Fig. 7, X, SW).

XI. The uppermost part of the ridge, just before it joins River Ridge, becomes slightly less steep, and has a deeper soil. The admixture of more mesophytic species, as sugar maple and cherry, in the chestnut forest, and the appearance of mesophytic (mull) herbaceous plants, as *Trillium grandiflorum*, *Disporum lanuginosum*, *Uvularia grandiflora*, and *Dentaria laciniata*, change the character of the ridge forest, bringing it into accord with the prevailing forests of the region. Neither change in direction of slope nor of steepness is sufficient to explain the increasing mesophytism. Again the delicate balance between factors—determining either oak-chestnut or mixed mesophytic forest—is demonstrated. At this higher elevation, increase in fog, decrease in temperatures, although slight, make possible the development of a phase of mixed mesophytic forest even on a ridge.

The Joe Day ridge merges with River Ridge, here the divide between Joe Day drainage and Colliers Creek drainage.

THE VALLEY OF JOE DAY BRANCH

The forest of the valley and valley slopes of Joe Day Branch does not change with minor variations in steepness or direction of slope. The influence of underlying rock is not discernible. Opposing valley slopes, except in the lowest part of the valley, are of course different, the left-hand (westerly) slope grading upward into ridge types of forest. The forest of the entire valley of Joe Day Branch and all its northwesterly slopes and the lower parts of its westerly slopes is mixed mesophytic, varying to some extent altitudinally (see chart, Fig. 10, and Table 3). For topography of area see map (Fig. 1) and profile (Fig. 2B).

I. In the mixed mesophytic forest of the lower valley, hemlock and beech are the two most important species, together comprising 45 percent of the canopy. *Rhododendron* is always abundant in the understory, especially near the stream, and in quantity generally extends higher on the westerly slopes. Where *Rhododendron* forms a definite layer, the herbaceous growth is sparse. Elsewhere the herbaceous layer is rich and varied although not as much so as in the higher forests.

Upslope (not upstream), this mixed forest merges with the hemlock-beech-oak or hemlock-chestnut-mixed mesophytic type of the lower spurs or ridges. Farther upstream, hemlock and *Rhododendron* become more limited in lateral extent, soon dropping out entirely.

AREA No. → No. of TREES	RAVINE SLOPES								HIGHER WESTERLY		
	I	II	III	IV	V	VI	VII	TOTAL	VIII	IX	X
	198	38	72	29	32	55	73	497%	36	162	42
<i>Acer saccharum</i> sugar maple								20.5			
<i>Tilia heterophylla</i> + basswood								12.1			
<i>Tsuga canadensis</i> hemlock								12.1			
<i>Aesculus octandra</i> buckeye								10.5			
<i>Fagus grandifolia</i> beech								9.0			
<i>Castanea dentata</i> chestnut								7.6			
<i>Liriodendron tulipifera</i> tulip tree								6.8			
<i>Acer rubrum</i> red maple								5.0			
<i>Quercus borealis maxima</i> red oak								4.8			
<i>Quercus alba</i> white oak								3.0			
<i>Nyssa sylvatica</i> sour gum								1.6			
<i>Betula allegheniensis</i> birch								1.2			
<i>Magnolia Fraseri</i> mountain magnolia								1.2			
<i>Magnolia acuminata</i> cucumber tree								1.0			
<i>Fraxinus biltmoreana</i> & ash. <i>F. americana</i>								.8			
<i>Juglans cinerea</i> butternut								.6			
<i>Carya ovata</i> shell-bark hickory								.6			
<i>Quercus montana</i> chestnut								.4			
<i>Carya</i> spp. hickory								.4			
<i>Juglans nigra</i> walnut								.4			
<i>Prunus serotina</i> wild black cherry								.2			
<i>Pinus echinata</i> yellow pine											

FIG. 10. Percentage composition of canopy of forest communities of the valley and valley slopes of Joe Day Branch.

II. Beech continues as an important species of the mixed mesophytic forest of the valley (now without hemlock), along with tulip tree, sugar maple, chestnut, buckeye, basswood, and a number of other species (Fig. 10). A larger variety and greater density of shrubs (other than *Rhododendron*) and herbaceous plants further distinguish this forest (Table 3).

III. Where the steeper slopes of the mountain begin (generally just below the 2,000-foot contour), the forest changes to a sugar maple-basswood-buckeye or sugar maple-basswood-buckeye-tulip tree type in which beech is

UNDERSTORY TREES	TREES								HERBS (cont.)	HERBS							
	I	II	III	IV	V	VI	VII	VIII		I	II	III	IV	V	VI	VII	VIII
Acer rubrum	X	X	X	X	X	X	X	X	Heracleum lanatum	X	X	X	X	X	X	X	X
Aesculus varus	X	X	X	X	X	X	X	X	Hesperis sp.	X	X	X	X	X	X	X	X
Aesculus cotinifera	X	X	X	X	X	X	X	X	Houstonia tenuiflora	X	X	X	X	X	X	X	X
Astilbe canadensis	X	X	X	X	X	X	X	X	Hydrophyllum canadense	X	X	X	X	X	X	X	X
Betula alleghaniensis	X	X	X	X	X	X	X	X	Impatiens pallida	X	X	X	X	X	X	X	X
Carpinus caroliniana	X	X	X	X	X	X	X	X	Iris cristata	X	X	X	X	X	X	X	X
Castanea dentata	X	X	X	X	X	X	X	X	Krigia amplexicaulis	X	X	X	X	X	X	X	X
Cercis canadensis	X	X	X	X	X	X	X	X	Laportea canadensis	X	X	X	X	X	X	X	X
Cornus florida	X	X	X	X	X	X	X	X	Millium canadense	X	X	X	X	X	X	X	X
Fagus grandifolia	X	X	X	X	X	X	X	X	Piparis illinoensis	X	X	X	X	X	X	X	X
Fraxinus sp. tulipifera	X	X	X	X	X	X	X	X	Physalis quadrifolia	X	X	X	X	X	X	X	X
Liriodendron maximiliani	X	X	X	X	X	X	X	X	Viola blanda	X	X	X	X	X	X	X	X
Maackia pinnatifida	X	X	X	X	X	X	X	X	Viola hastata	X	X	X	X	X	X	X	X
Malus sp.	X	X	X	X	X	X	X	X	Viola papilionacea	X	X	X	X	X	X	X	X
Nyssa sylvatica	X	X	X	X	X	X	X	X	Viola rotundifolia	X	X	X	X	X	X	X	X
Ostrya virginiana	X	X	X	X	X	X	X	X	Viola scaberrima	X	X	X	X	X	X	X	X
Oxydendrum arboreum	X	X	X	X	X	X	X	X	Viola Stoneana	X	X	X	X	X	X	X	X
Prunus serotina	X	X	X	X	X	X	X	X	Viola sp.	X	X	X	X	X	X	X	X
Quercus borealis maxima	X	X	X	X	X	X	X	X									
Quercus montana	X	X	X	X	X	X	X	X									
Robinia pseudo-acacia	X	X	X	X	X	X	X	X									
Salix nigricans	X	X	X	X	X	X	X	X									
Tilia heterophylla	X	X	X	X	X	X	X	X									
Tilia canadensis	X	X	X	X	X	X	X	X									
SHRUBS & WOODY CLIMBERS																	
Aristolochia macrophylla	X	X	X	X	X	X	X	X	Thalictrum dioicum	X	X	X	X	X	X	X	X
Benzoin aestivale	X	X	X	X	X	X	X	X	Thalictrum pinnatifidum	X	X	X	X	X	X	X	X
Cornus alternifolia	X	X	X	X	X	X	X	X	Thalictrum triflorum	X	X	X	X	X	X	X	X
Hamamelis virginiana	X	X	X	X	X	X	X	X	Violaria grandiflora	X	X	X	X	X	X	X	X
Hydrangea macrophylla	X	X	X	X	X	X	X	X	Violaria perfoliata	X	X	X	X	X	X	X	X
Hydrangea paniculata	X	X	X	X	X	X	X	X	Viola blanda	X	X	X	X	X	X	X	X
Passiflora guianensis	X	X	X	X	X	X	X	X	Viola hastata	X	X	X	X	X	X	X	X
Pyrola puberula	X	X	X	X	X	X	X	X	Viola papilionacea	X	X	X	X	X	X	X	X
Rhododendron (Azalea)	X	X	X	X	X	X	X	X	Viola rotundifolia	X	X	X	X	X	X	X	X
calendulaceae	X	X	X	X	X	X	X	X	Viola scaberrima	X	X	X	X	X	X	X	X
Rhododendron (Azalea), red	X	X	X	X	X	X	X	X	Viola Stoneana	X	X	X	X	X	X	X	X
Rhododendron maximum	X	X	X	X	X	X	X	X									
Rhus Toxicodendron	X	X	X	X	X	X	X	X									
Rubus sp.	X	X	X	X	X	X	X	X									
Vaccinium spp.	X	X	X	X	X	X	X	X									
Vaccinium acerifolium	X	X	X	X	X	X	X	X									
Vitis sp.	X	X	X	X	X	X	X	X									
GROUND HERBS																	
Epigaea repens	X	X	X	X	X	X	X	X									
Galax aphylla	X	X	X	X	X	X	X	X									

TABLE 3. Undergrowth of forest communities of valley and valley slopes of Joe Day Branch, Fig. 10.

a minor constituent (generally not over 10 percent). Higher, except on warmer slopes, beech soon drops out, and sugar maple, basswood, and buckeye are correspondingly more important. The extreme mesophytism of the forest is emphasized by the luxuriance and beauty of the vernal herbaceous layer. Rock slabs, if present, are covered with vegetation, for as little as two inches of humus soil over the rock is sufficient to support *Phacelia*, *Trillium*, *Dicentra*—any of the most mesophytic of forest herbs.

IV. On westerly slopes the undergrowth is not quite so dense, there is more dogwood, less buckeye or none at all. Rock slabs have patches of



FIG. 11. Red oak (nearly 4 feet in diameter breast high) in the sugar maple-basswood-buckeye forest of area *IV* of Joe Day Branch. May 6.

Sedum and mosses instead of the delicate mesophytic herbs. The forest is another variant (segregate) of the mixed mesophytic with an increased percentage of sugar maple, chestnut, and in places, of tulip tree and oak, and a decrease in basswood and buckeye (compare with area *V*, *Nb* on Fig. 7).

Higher on the westerly slope (higher above creek) this forest gives way to the chestnut oak-chestnut ridge or dry slope type (area *VIII* in Fig. 10).

V, *VI*, *VII*. The next thousand feet of elevation on the northerly slopes is remarkably uniform, not only in the drainage basin of Joe Day Branch,



FIG. 12. The sugar maple-basswood-buckeye forest of area *VII*, Joe Day Branch, showing wealth of vernal flora; Trilliums most conspicuous. The two nearer trees are sugar maples with buckeye and basswood in middle distance. May 6.

but also wherever examined. Three areas on Joe Day, counted separately, are shown in columns *V*, *VI*, and *VII* of the chart (Fig. 10). The dominance of sugar maple, basswood, and buckeye is evident. The herbaceous layer is continuous and luxuriant, comprising a great variety of showy vernal plants and of ferns (Fig. 13). There is generally an increase in *Trillium erectum*. *Disporum maculatum* is a distinctive plant of this forest community.

This sugar maple-basswood-buckeye forest is, areally, one of the most important association-segregates of the mixed mesophytic forest of the Cumberland Mountains. It is made up of magnificent trees with tall columnar trunks, many three feet or more in diameter breast high (Figs. 11, 12). The floral display early in May is unsurpassed. In spite of the exceedingly steep slope generally prevailing at these elevations on Black Mountain, there is a deep mull humus layer, a reflection of the kinds of canopy trees, and in turn largely responsible for the luxuriance of the herbaceous vegetation.



FIG. 13. Early in May, the mountain slopes in the sugar maple-basswood-buckeye forest are a veritable flower garden. Large white *Trillium grandiflorum*, both red and yellow *Trillium erectum*, *Delphinium tricorne*, *Stellaria pubera*, and *Disporum maculatum* contribute to the floral display. Uncurling fern fronds at base of large buckeye tree. (Area *VII*, Joe Day Branch.)

IX. Toward the head of the valley, the westerly (left-hand) slope is a mixed forest in which chestnut and chestnut oak dominate (Fig. 14). The contrast of slopes, early in May, is extreme. The westerly slope is brown with leaf litter, the herbaceous plants are few and scattered, the heath layer, especially *Kalmia*, prominent, the chestnut and oak canopy is not yet in

leaf, the whole slope is bathed in sunlight. The northerly (right-hand) slope is covered by a rich green ground cover, heaths are absent, the early leafing of the three dominants of the canopy makes this slope green and shaded. Even in summer, when there are more herbaceous plants on the westerly slope and all trees are in leaf, the contrast of slopes is great due to the great species differences.

X. Near the mountain top on the westerly slope, the forest is dominantly chestnut and grades into typical ridge type forest of the mountain summit (*R* in Fig. 20).



FIG. 14. The chestnut oak-chestnut forest of the higher westerly slopes of Joe Day Branch (area IX) with *Kalmia* prominent in the undergrowth.

Viewed in its entirety, the basin of Joe Day Branch is covered by mixed mesophytic forest limited on the encircling ridge tops and high westerly and southwesterly slopes by oak-chestnut forest, and, on the narrow ridge between its two forks, interrupted by a narrow tongue of oak-chestnut forest which there descends to within a few hundred feet of creek level. This distribution of major forest communities is particularly noticeable in early May, for then the oak-chestnut forest is almost leafless and all communities of the mixed mesophytic forest are green.

STAGGERWEED HOLLOW

Staggerweed Hollow, a narrow ravine with steep gradient, trends in a north-northwest direction at the western margin of the area included in the map (Fig. 1). Its upper slopes (above about 2,000 feet) are clothed with the sugar maple-basswood-buckeye type of forest seen in comparable situations in Joe Day Branch. No counts of this are included here. The forest of the lower part of Staggerweed Hollow and of its westerly slopes up to about 2,000 feet is included for comparison with the forests of the Joe Day basin (Fig. 15 and Table 4).

The ravine forests (I and II of chart, Fig. 15) may be compared with the lower forest communities of Joe Day Branch. Beech is relatively more important in Staggerweed than in Joe Day. Only on the valley slopes somewhat open to the west (areas V, VI) is hemlock an important species. In both valleys, sugar maple increases part way up. In both, *Rhododendron* is important in the lower part of the ravine. These lower forests in both streams belong to the beech-hemlock mixed mesophytic type.

The upper lateral westerly slope forests (III, V, and VI of chart, Fig. 15) are comparable to the forests of similar

AREA No.→ No. of TREES	I	II	III	IV	V	VI	TOTAL exc. IV
	90	78	120	34	34	35	357 %
<i>Fagus grandifolia</i> beech							33.3
<i>Tsuga canadensis</i> hemlock							9.0
<i>Liriodendron tulipifera</i> tulip tree							8.4
<i>Quercus alba</i> white oak							7.3
<i>Tilia heterophylla</i> + basswood							7.0
<i>Castanea dentata</i> chestnut							6.2
<i>Acer saccharum</i> sugar maple							5.3
<i>Acer rubrum</i> red maple							4.5
<i>Quercus borealis maxima</i> red oak							3.1
<i>Aesculus octandra</i> buckeye							3.1
<i>Nyssa sylvatica</i> sour gum							3.1
<i>Betula allegheniensis</i> birch							2.8
<i>Quercus montana</i> chestnut oak							1.9
<i>Magnolia Fraseri</i> mountain magnolia							1.4
<i>Carya</i> spp. hickory							1.1
<i>Fraxinus biltmoreana</i> ash							1.1
<i>Magnolia acuminata</i> cucumber tree							.6
<i>Juglans nigra</i> walnut							.6
<i>Carya ovata</i> shell-bark hickory							.3
<i>Quercus coccinea</i> scarlet oak							
<i>Pinus echinata</i> yellow pine							

FIG. 15. Percentage composition of canopy of forest communities of Staggerweed Hollow.

UNDERSTORY TREES	I	II	III	IV	V	VI
<i>Acer rubrum</i>			X			
<i>Acer saccharum</i>		X				
<i>Aesculus octandra</i>		X				
<i>Aselanchier canadensis</i>				X	X	
<i>Betula allegheniensis</i>	X					
<i>Carpinus caroliniana</i>	X	X	X			
<i>Castanea dentata</i>			X	X		
<i>Cornus florida</i>			X	X		
<i>Fagus grandifolia</i>		X	X		X	X
<i>Fraxinus</i> sp.	X					
<i>Juglans cinerea</i>	X					
<i>Juglans nigra</i>		X				
<i>Liriodendron tulipifera</i>	X				X	
<i>Magnolia acuminata</i>	X					
<i>Magnolia Fraseri</i>	X	X	X			
<i>Nyssa sylvatica</i>			X			
<i>Oxydendrum arboreum</i>			X	X	X	
<i>Quercus alba</i>			X			X
<i>Quercus borealis maxima</i>			X			
<i>Quercus montana</i>			X	X		
<i>Robinia Pseudo-Acacia</i>			X	X		
<i>Tilia heterophylla</i>		X				
<i>Tsuga canadensis</i>	X	X		X	X	
SHRUBS & WOODY CLIMBERS						
<i>Benzoin aestivale</i>	X					
<i>Hamelis virginiana</i>	X	X				
<i>Hydrangea arborescens</i>	X					
<i>Kalmia latifolia</i>			X	X		
<i>Paedera quinquefolia</i>			X			
<i>Pyrolaria pubera</i>			X			
<i>Rhododendron (Azalea), red</i>			X			
<i>Rhododendron maximum</i>	X		X	X	X	X
<i>Rhus Toxicodendron</i>	X					
<i>Vaccinium corymbosum</i>			X	X		
<i>Silax Bona-nox</i>			X			
<i>Viburnum acerifolium</i>			X			
<i>Vitis bicolor</i>			X			
GROUND HEATHS						
<i>Chimaphila maculata</i>			X			
<i>Epigaea repens</i>				X		
<i>Galax aphylla</i>			X	X	X	
<i>Gaultheria procumbens</i>			X	X		
FERNS						
<i>Adiantum pedatum</i>	X	X	X			
<i>Aspidium Goldianum</i>	X	X				
<i>Aspidium marginale</i>			X			
<i>Aspidium noveboracense</i>			X			
<i>Asplenium acrostichoides</i>	X	X				
<i>Asplenium angustifolium</i>	X	X				
<i>Phlegopteris hexagonoptera</i>	X	X				
<i>Polystichum acrostichoides</i>	X		X			
HERBS	I	II	III	IV	V	VI
<i>Aspicarpa monoica</i>	X					
<i>Anemone virginiana</i>			X			
<i>Anemone thalictroides</i>			X			
<i>Arisaema triphyllum</i>	X		X			
<i>Aristolochia Serpentina</i>			X			
<i>Asarum canadense</i>	X	X				
<i>Aster cordifolius</i>			X			
<i>Aster divaricatus</i>			X			
<i>Astilbe biternata</i>	X	X				
<i>Campanula americana</i>		X				
<i>Carex laxiflora latifolia</i>		X				
<i>Caulophyllum thalictroides</i>	X	X				
<i>Cimicifuga racemosa</i>	X	X				
<i>Cimicifuga racemosa cordifolia</i>						
<i>Clintonia umbellulata</i>			X		X	
<i>Cypripedium parviflorum pubescens</i>			X			
<i>Delphinium tricornis</i>		X				
<i>Desmodium pauciflorum</i>			X			
<i>Dioscorea villosa</i>			X			
<i>Epipactis pubescens</i>			X			
<i>Geranium maculatum</i>	X	X				
<i>Heuchera longiflora</i>			X			
<i>Houstonia tenuiflora</i>			X			
<i>Hybanthus concolor</i>			X			
<i>Hydrophyllum canadense</i>	X	X				
<i>Impatiens pallida</i>	X	X				
<i>Laportea canadensis</i>	X	X				
<i>Liparis liliifolia</i>			X			
<i>Medeola virginiana</i>			X			
<i>Mitchella repens</i>			X	X	X	
<i>Monotropa uniflora</i>			X			
<i>Osmorhiza longistylis</i>			X			
<i>Pedicularis canadensis</i>			X			
<i>Phacelia bipinnatifida</i>	X	X				
<i>Podophyllum peltatum</i>	X	X				
<i>Polygonatum commutatum</i>	X	X				
<i>Polygonum virginianum</i>	X	X				
<i>Ranunculus hispidus</i>			X			
<i>Ranunculus recurvatus</i>	X	X				
<i>Sanguinaria canadensis</i>		X				
<i>Sedum ternatum</i>		X	X			
<i>Senecio obovatus</i>		X	X			
<i>Smilacina racemosa</i>		X				
<i>Solidago latifolia</i>		X				
<i>Steironema intermedium</i>			X			
<i>Stellaria pubera</i>		X	X			
<i>Thaspium aureum atropurpureum</i>			X			
<i>Tiarella cordifolia</i>	X	X				
<i>Trillium grandiflorum</i>		X				
<i>Trillium erectum</i>	X	X				
<i>Uvularia grandiflora</i>		X				
<i>Uvularia perfoliata</i>		X				
<i>Viola blanda</i>	X					
<i>Viola canadensis</i>		X				
<i>Viola hastata</i>			X			

TABLE 4. Undergrowth of forest communities of Staggerweed Hollow, Fig. 15.

elevations on the slopes of Joe Day ridge, especially to area V and its adjacent southwesterly slope forests (Fig. 7). The dominance of beech (in area III) with chestnut second in importance and the absence of three important mesophytic species—sugar maple, basswood and buckeye—is the most significant feature of these westerly slope forests. The beech forest (beech-chestnut or beech-hemlock) with ericaceous layer is a striking feature of the lower westerly (drier) slopes of Black Mountain.

The chestnut oak-chestnut ridge forest (area IV) with *Kalmia-Rhododendron* layer is comparable to III of the Joe Day ridge transect.

MEETING HOUSE BRANCH

Meeting House Branch flows in a northerly direction just to the north of Joe Day Branch (see map, Fig. 1). A short stream, entirely below 2,200 feet, its valley slopes display none of the higher altitude features, none of

the sugar maple-basswood-buckeye forest. The ridge separating Meeting House Branch from its right fork trends in an almost north direction. Because of the narrowness of the valley and its direction, and the northerly slope of the ridge, it is desirable to compare the forests (Figs. 16, 17; Tables 5, 6) with the forests of Joe Day Branch (Fig. 10, Table 3), Joe Day ridge (Fig. 5, Table 1), and Staggerweed Hollow (Fig. 15, Table 4).

Ravine Slopes

The forest of the ravine and its adjacent slopes is similar to the corresponding areas of Joe Day Branch and of Staggerweed Hollow. Only one community is distinguished in the ravine (*Ra* of Fig. 16 and Table 5) which is comparable to area *I* of Joe Day Branch and of Staggerweed Hollow. The abundance of *Rhododendron*, the ferns, and the wealth of herbaceous growth further emphasize the similarity—the essential uniformity—of the forests of the lower parts (altitudinally) of valleys of the region.

The westerly slope forest above this mixed mesophytic forest differs from the forest of the corresponding area of Staggerweed Hollow in the absence of or unimportance of beech, and in the greater importance of hemlock and of white oak (areas *W1*, *W2*, *W3* of Fig. 16). The dominance of the evergreen heath shrubs, *Rhododendron* and *Kalmia*, accounts in part for the sparse tree reproduction and paucity of ground layer plants, other than ericads and species which find the deep hemlock and ericaceous duff favorable.

The easterly slope forest is mixed mesophytic (both in canopy and undergrowth), with beech the most important species. Areas *E1* and *E2* show the sequence up-slope from ravine to area *II* of the ridge; areas *E3* and *E4*, from ravine to area *IV* of ridge (Fig. 17). In areas *E1* and *E2*, *Rhododendron* and *Kalmia*, respectively, form a broken lower layer. The forest is the beech-heath type more generally found on westerly slopes.

Meeting House Branch Ridge Transect

The Meeting House Branch ridge transect follows the ridge crest from the flat bordering the Cumberland River at about 1,600 feet to the place where the ridge merges with the mountain slope at 2,300 feet, about three fourths of a mile (Figs. 2C, 17; Table 6).

The forest of the lowest slope is beech-hemlock-tulip tree with a *Rhododendron* layer (not shown on chart, as not intact). Higher (area *I*), hemlock and chestnut are codominant, each forming approximately 30 percent of the canopy.

A very steep ascent leads up to a sandstone outcrop (at about 1,750 feet) which forms something of a ledge or projecting rocky point on the ridge. Chestnut with an undergrowth of *Rhododendron* formerly occupied the steep slope; now small scarlet oaks are replacing the chestnut.

AREA No. → No. of TREES	WEST SLOPE					EAST SLOPE					TOTAL M.M.:
	Ra	W1	W2	W3	W 1-3	E1	E2	E3	E4	E 1-4	Ra + W1 + E1 - 4
	108	38	32	33	103	26	10	19	23	78	224 %
<i>Tsuga canadensis</i> hemlock											28.1
<i>Fagus grandifolia</i> beech											24.1
<i>Quercus alba</i> white oak											8.9
<i>Castanea dentata</i> chestnut											7.6
<i>Acer rubrum</i> red maple											5.4
<i>Liriodendron tulipifera</i> tulip tree											4.9
<i>Carya</i> spp. hickory											4.9
<i>Tilia heterophylla</i> + basswood											3.1
<i>Quercus borealis maxima</i> red oak											2.7
<i>Betula allegheniensis</i> birch											2.2
<i>Magnolia Fraseri</i> mountain magnolia											2.2
<i>Acer saccharum</i> sugar maple											1.8
<i>Nyssa sylvatica</i> sour gum											1.8
<i>Juglans cinerea</i> butternut											.9
<i>Aesculus octandra</i> buckeye											.5
<i>Juglans nigra</i> black walnut											.5
<i>Quercus montana</i> chestnut oak											.5
<i>Quercus coccinea</i> scarlet oak											
<i>Quercus velutina</i> black oak											
<i>Pinus rigida</i> pitch pine											

FIG. 16. Percentage composition of canopy of forest communities of Meeting House Branch. Divided so as to show ravine forest (Ra) and forests of opposing east and west slopes.

The relatively gentle slope of the ridge crest above this outcrop (area II) is essentially chestnut forest with a *Kalmia* layer, while the steep side slopes of the ridge (area E2) support the beech-heath community.

The slope of the ridge crest rises rapidly but not uniformly above area II to about 2,000 feet. This steep slope (area III) supports a mixed forest in which red maple, white oak, chestnut, and hemlock are most important. The hemlock, however, is localized on one of the steepest parts of the ridge crest—the highest place, altitudinally, at which it occurs in this transect.

UNDERSTORY TREES	Ra	W1	W2	W3	E1	E2	E3	E4
Acer rubrum	X		X	X				X
Acer saccharum					X			X
Aesculus octandra	X							
Betula allegheniensis	X				X			
Carpinus caroliniana	X						X	
Carya sp.					X			X
Castanea dentata		X	X	X				
Cercis canadensis					X			
Cornus florida					X			
Fagus grandifolia	X						X	X
Fraxinus sp.								
Liriodendron tulipifera	X							
Magnolia Fraseri		X						
Nyssa sylvatica		X	X	X				
Oxydendrum arboreum		X	X	X				
Quercus alba			X					
Quercus coccinea			X					
Tilia heterophylla	X						X	
Tsuga canadensis	X	X						
SHRUBS AND WOODY CLIMBERS								
Benzoin aestivale								X
Castanea pumila				X				
Evonymus americanus	X							
Hamelis virginiana			X	X	X			
Hydrangea arborescens	X		X	X	X			
Kalmia latifolia			X	X	X			
Paedera quinquefolia						X		
Pyrolaria pubera					X			
Rhododendron maximum	X	X	X	X	X			
Rhus Toxicodendron					X			
Viburnum acerifolium								X
GROUND HEATHS								
Chimaphila maculata								X
Epigaea repens				X				
Galax aphylla		X	X	X	X			
Gaultheria procumbens			X	X	X			

TABLE 5. Undergrowth of forest communities of Meeting House Branch, Fig. 16.

Starting at about 2,000 feet, is a long relatively gentle rise (area IV'). Here is situated the most mesophytic of the ridge crest forests, a mixed forest definitely belonging to the mixed mesophytic association (see area IV', Fig. 17). The humus layer is of the mull type, the herbaceous vegetation in consequence rich and varied, distinctly of the mixed mesophytic aspect (see Table 6).

FERNS	Ra	W1	W2	W3	E1	E2	E3	E4
Adiantum pedatum								X
Aspidium novaeboracense		X						X
Aspidium spinulosum, var.	X							
Asplenium acrostichoides	X							X
Asplenium angustifolium	X							
Asplenium arnustum	X				X			
Phlegopteris hexagonoptera	X							X
Polystichum acrostichoides	X						X	X
HERBS								
Amphicarpa monoica	X							
Anemone virginiana	X							
Arisaema triphyllum	X							X
Aristolochia Serpentaria								X
Asarum virginicum	X							
Aster divaricatus							X	
Astilbe biternata							X	X
Cimicifuga racemosa					X		X	X
Cimicifuga racemosa cordifolia								X
Circaea alpina	X							
Conopholis americana								X
Cypripedium acaule			X	X				
Dentaria diphylla	X							
Dioscorea villosa								X
Disporum lanuginosum								X
Epipactis pubescens								X
Geranium maculatum	X					X		X
Hepatica acutiloba	X							
Impatiens pallida	X							
Laportea canadensis	X							X
Medeola virginiana	X							
Mitchella repens	X	X						
Monotropa uniflora					X			
Osmorhiza Claytani	X							
Sanguinaria canadensis	X							X
Smilacina racemosa						X		
Solidago latifolia	X							X
Stellaria pubera								X
Tiarella cordifolia	X							
Trillium grandiflorum	X						X	
Viola blanda	X						X	
Viola rotundifolia	X							

Above this, the slopes rise steeply, and the chestnut-chestnut oak type of forest begins, at first with a mixture of mesophytic species (area *V*). Beech drops out in the lower part of this rise, reaching on the ridge crest, an elevation close to 2,200 feet, a little lower than on the drier, sunnier Joe Day ridge. Higher, as the ridge crest becomes just a convexity of the steep mountain slope, the mesophytic species drop out and pines enter (area *VI*). On a rocky knob, a scarlet oak-pine community locally interrupts the oak-chestnut forest.

This ridge contrasts strongly with the Joe Day ridge in the importance of white oak; in the greater height to which hemlock ascends as an important constituent of the forest; in the absence from most parts of the ridge, and relative unimportance throughout, of chestnut oak (which totals only 4 percent of this ridge forest as contrasted with 19 percent of the same altitudinal part of the Joe Day ridge); and in the greater admixture of mesophytic species. The greater mesophytism of Meeting House Branch ridge is further emphasized by the herbaceous layer which (especially in area *IV*) contains a variety of typical mesophytic plants. Locally on both ridges, heaths dominate in both shrub and ground layers.

AREA No.→ No. of TREES	I	II	III	IV	V	VI	TOTAL I-IV
	63	21	32	44	15	24	160 %
<i>Castanea dentata</i> chestnut							26.3
<i>Quercus alba</i> white oak							17.5
<i>Tsuga canadensis</i> hemlock							14.4
<i>Acer rubrum</i> red maple							6.9
<i>Carya</i> spp. hickory							6.9
<i>Fagus grandifolia</i> beech							5.6
<i>Nyssa sylvatica</i> sour gum							5.6
<i>Acer saccharum</i> sugar maple							4.4
<i>Quercus coccinea</i> scarlet oak							4.4
<i>Robinia Pseudo-Acacia</i> black locust							2.5
<i>Liriodendron tulipifera</i> tulip tree							1.9
<i>Magnolia Fraseri</i> mountain magnolia							1.2
<i>Tilia heterophylla</i> basswood							.6
<i>Quercus borealis maxima</i> red oak							.6
<i>Magnolia acuminata</i> cucumber tree							.6
<i>Quercus velutina</i> black oak							.6
<i>Quercus montana</i> chestnut oak							
<i>Pinus rigida</i> pitch pine							
<i>Pinus echinata</i> yellow pine							

FIG. 17. Percentage composition of canopy of forest communities of Meeting House Branch ridge transect. This is comparable in elevation to areas *I* to *VI*, inclusive, of the Joe Day ridge transect; note contrast in amount of chestnut oak on the two ridges.

UNDERSTORY TREES	I	II	III	IV	V	VI
<i>Acer pennsylvanicum</i>				X	X	
<i>Acer rubrum</i>	X			X	X	
<i>Acer saccharum</i>			X	X	X	
<i>Amelanchier canadensis</i>	X					X
<i>Betula allegheniensis</i>				X		
<i>Carpinus caroliniana</i>			X	X		
<i>Carya alba</i>				X		
<i>Carya glabra</i>		X	X	X	X	
<i>Castanea dentata</i>	X	X		X	X	X
<i>Cercis canadensis</i>				X		
<i>Cornus florida</i>			X	X	X	X
<i>Fagus grandifolia</i>	X			X	X	
<i>Liriodendron tulipifera</i>						X
<i>Magnolia acuminata</i>				X	X	
<i>Magnolia Fraseri</i>	X		X	X		
<i>Nyssa sylvatica</i>			X			
<i>Ostrya virginiana</i>			X	X	X	
<i>Oxydendrum arboreum</i>	X	X	X	X		
<i>Prunus serotina</i>				X		
<i>Quercus alba</i>	X	X	X	X		
<i>Quercus borealis maxima</i>				X	X	
<i>Quercus coccinea</i>	X	X				
<i>Quercus montana</i>				X	X	
<i>Sassafras variifolium</i>				X		
<i>Tsuga canadensis</i>	X		X			
SHRUBS & WOODY CLIMBERS						
<i>Cornus alternifolia</i>				X		
<i>Corylus americana</i>			X	X		
<i>Hamamelis virginiana</i>	X	X	X			X
<i>Kalmia latifolia</i>	X	X				X
<i>Paederia quinquefolia</i>			X	X		
<i>Pyrularia pubera</i>	X		X			
<i>Rhododendron (Azalea), red</i>					X	
<i>Rhododendron maximum</i>	X	X	X		X	
<i>Rhus Toxicodendron</i>			X	X	X	
<i>Smilax Bona-nox</i>				X		
<i>Vaccinium corymbosum</i>				X	X	
<i>Viburnum acerifolium</i>				X		
<i>Vitis sp.</i>				X	X	
GROUND HEATHS						
<i>Chimaphila maculata</i>				X	X	X
<i>Epigaea repens</i>	X					X
<i>Galax aphylla</i>	X	X				X
<i>Gaultheria procumbens</i>	X	X				X
FERNS	I	II	III	IV	V	VI
<i>Adiantum pedatum</i>			X	X		
<i>Aspidium noveboracense</i>			X	X		
<i>Aspidium marginale</i>			X	X		
<i>Botrychium virginianum</i>				X		
<i>Phegopteris hexagonoptera</i>				X		
<i>Polypodium virginianum</i>	X					
<i>Polystichum acrostichoides</i>			X	X		X
HERBS						
<i>Amphicarpa monoica</i>				X		
<i>Anemone thalictroides</i>					X	
<i>Aristolochia Serpentaria</i>				X		
<i>Asarum virginicum</i>	X					
<i>Astilbe biternata</i>				X		
<i>Caulophyllum thalictroides</i>				X		
<i>Cimicifuga racemosa</i>			X	X	X	
<i>Cimicifuga racemosa cordifolia</i>					X	
<i>Desmodium nudiflorum</i>				X	X	
<i>Disporum lanuginosum</i>				X	X	
<i>Disporum maculatum</i>				X		
<i>Epipactis pubescens</i>				X		
<i>Galium lanceolatum</i>				X		
<i>Gentiana sp.</i>	X					
<i>Geranium maculatum</i>			X	X		
<i>Heuchera longiflora</i>				X	X	
<i>Houstonia tenuiflora</i>				X	X	X
<i>Nedoclea virginiana</i>		X	X			
<i>Microstylis unifolia</i>						X
<i>Mitchella repens</i>			X			
<i>Oxalis grandis</i>				X		
<i>Phryma leptostachya</i>				X		
<i>Pogonia verticillata</i>	X	X				
<i>Silene stellata</i>				X		
<i>Smilacina racemosa</i>				X		
<i>Solidago caesia</i>			X	X	X	
<i>Stellaria pubera</i>			X			
<i>Thaspium aureum</i>			X	X		
<i>Thaspium atropurpureum</i>			X	X		
<i>Tiarella cordifolia</i>			X			
<i>Trillium grandiflorum</i>			X	X		
<i>Uvularia perfoliata</i>				X		
<i>Vicia caroliniana</i>				X		
<i>Viola blanda</i>			X			
<i>Viola palmata</i>				X		

TABLE 6. Undergrowth of forest communities of Meeting House Branch ridge, Fig. 17.

COMMUNITIES OF THE SOUTHERLY SLOPE

The study of the southerly slope embraces: (1) the communities of a convex slope facing south; (2) communities of a ravine or concavity of slope; and (3) communities in the upper Left Fork of Colliers Creek (for location see map, Fig. 1). The general aspect of the area where the south slope studies were made is shown in Fig. 4.

SOUTH SLOPE TRANSECT

The transect on the convex slope rises from the Left Fork of Colliers Creek at 2,000 feet, meeting the crest of River Ridge at 3,200 feet, at a point near the upper terminus of the Joe Day ridge transect. The south slope rises steeply, with an average rise of nearly one foot in two (Fig. 2D). On such a steep slope exposed directly to the sun the surface soil is dried rapidly and humus decomposition is interfered with. These effects are increased by the late spring leafing of south slope dominants, for hot days of April

and early May are sunny days in south slope woods. The failure of deep humus accumulation and the absence of lime-increasing leaf litters⁵ tend to accentuate the minor differences of underlying rock. Outcropping sandstone strata, and large slabs lying on the surface, are not covered with humus as on northerly slopes, but remain bare or support only xerophytic mosses and lichens, species of *Thuidium*, *Hedwigia*, *Parmelia*, and *Physcia*, while the ledges above such strata are good heath habitats and generally support *Kalmia* thickets. Oaks are important throughout the south slope forest (except at its base), white oak at low elevations, chestnut oak elsewhere (Fig.

AREA No → No. of TREES	I	II	III	IV	V	VA	VI	VII	VIII	TOTAL exc. VA
	20	22	17	24	21	21	14	9	15	142%
<i>Quercus montana</i> chestnut oak										36.6
<i>Castanea dentata</i> chestnut										29.5
<i>Quercus alba</i> white oak										16.2
<i>Liriodendron tulipifera</i> tulip tree										3.5
<i>Acer rubrum</i> red maple										3.5
<i>Quercus borealis maxima</i> red oak										2.8
<i>Quercus velutina</i> black oak										2.1
<i>Nyssa sylvatica</i> sour gum										2.1
<i>Fagus grandifolia</i> beech										1.4
<i>Magnolia acuminata</i> cucumber tree										1.4
<i>Robinia Pseudo-Acacia</i> black locust										.7
<i>Carya ovata</i> shell-bark hickory										
<i>Carya</i> spp. hickory										
<i>Acer saccharum</i> sugar maple										

FIG. 18. Percentage composition of canopy of forest communities of transect on south slope of River Ridge.

I. The lower slope forest contains a high proportion of white oak. In some places along Colliers Creek, beech, or beech and hemlock, mingle with the white oak on the lower slopes. In the area traversed by the transect, chestnut is second to white oak in importance. A sandy soil reflects the nature of underlying rock and is in turn responsible for the heaths of the shrub layer and the character of the sparse herbaceous layer.

II. Upward, chestnut and chestnut oak increase, although white oak and an admixture of mesophytic species still remain in canopy and understory.

III. An outcrop of massive sandstone is marked by a dense *Kalmia-Vaccinium* belt along the top of the outcrop, and an increase in the proportion of chestnut oak in the canopy—due to shallow soil over rock.

IV. White oak decreases rapidly, reaching here its upper altitudinal limits. The increase in chestnut and tulip tree is a reflection of deeper soil on a slightly less steep part of the slope. The differences are not sufficient to be reflected in the undergrowth, which continues as lower on the slope.

⁵ See effect of sugar maple and basswood leaves discussed by Alway, Kittredge, and Methley (1933) and Alway, Methley, and Younge (1933).

18 and Table 7). At the base of the slope, in the valley of the Left Fork of Colliers Creek, is a mixed mesophytic forest—the mixed type, including hemlock.

UNDERSTORY TREES										HERBS									
I	II	III	IV	V	VI	VII	VIII	IX	X	I	II	III	IV	V	VI	VII	VIII	IX	X
<i>Acer rubrum</i>	X	X		X															
<i>Acer saccharum</i>																			
<i>Amelanchier canadensis</i>	X	X								X									
<i>Carya ovata</i>	X	X	X							X									
<i>Castanea dentata</i>	X	X	X	X						X									
<i>Cercis canadensis</i>	X	X	X	X						X									
<i>Cornus florida</i>	X	X	X	X						X									
<i>Fagus grandifolia</i>	X	X	X	X						X									
<i>Liriodendron tulipifera</i>	X	X	X	X						X									
<i>Magnolia acuminata</i>	X	X	X	X						X									
<i>Magnolia fraseri</i>	X	X	X	X						X									
<i>Oxydendrum arboreum</i>	X	X	X	X						X									
<i>Quercus alba</i>	X	X	X	X						X									
<i>Quercus montana</i>	X	X	X	X						X									
<i>Sassafras variifolium</i>	X	X	X	X						X									
<i>Tsuga canadensis</i>	X																		
SHRUBS & WOODY CLIMBERS																			
<i>Hamamelis virginiana</i>	X	X	X	X	X					X									
<i>Kalmia latifolia</i>	X	X	X	X	X					X									
<i>Paederia quinquefolia</i>	X	X	X	X	X					X									
<i>Pyrola puberula</i>	X	X	X	X	X					X									
<i>Rhododendron (Azalea), red</i>	X	X	X	X	X					X									
<i>Rhododendron maximum</i>	X	X	X	X	X					X									
<i>Smilax Bona-nox</i>	X	X	X	X	X					X									
<i>Vaccinium corymbosum</i>	X	X	X	X	X					X									
<i>Vaccinium stamineum</i>	X	X	X	X	X					X									
<i>Vaccinium vacillans</i>	X	X	X	X	X					X									
<i>Viburnum acerifolium</i>	X	X	X	X	X					X									
<i>Vitis sp.</i>	X									X									
GROUND HEATHS																			
<i>Chimaphila maculata</i>	X									X									
FERNS																			
<i>Adiantum pedatum</i>										X									
<i>Aspidium marginale</i>										X									
<i>Polystichum acrostichoides</i>	X	X								X									

TABLE 7. Undergrowth of forest communities of south slope of River Ridge, Fig. 18.

V. Ascending to a very rocky part of the slope, chestnut oak assumes dominance. Except for *Kalmia*, the undergrowth is exceedingly poor—almost nothing except *Heuchera longiflora* among the rocks.

VA. That slight changes in direction and contour of slope are as important here as on ridges of the northwesterly slope of the mountain is evident at this place, where the course followed approaches the borders of a slight

concavity of slope. A southwesterly slope, slightly concave instead of convex, supports a mesophytic forest from which chestnut oak is absent, and in which there is a marked increase in herbaceous ground cover, apparent in the broken green carpet.

VI. Locally, chestnut is dominant and chestnut oak plays a minor rôle. As standing dead chestnut is counted just as are living trees of the canopy, the picture of percentage is that which prevailed prior to 1932, the year when the effect of chestnut blight first became evident in this region. In the few years that have intervened, secondary growth has not been rapid on south slopes. The undergrowth of these south slope forests is in all places very open. Seedling chestnut oaks are very numerous. *Kalmia* and *Smilax* have increased in vigor due to increased light.

VII. Higher, this part of the south slope assumes more of a ridge aspect, becomes very rocky with outcropping ledges. Crooked chestnut oak forms an open canopy beneath which is a dense *Kalmia* heath. The ledges so apparent here in the ridge appear at intervals horizontally along the face of the south slope where the forest in a band is prevailingly chestnut oak. The route followed is shifted laterally at this place so as to include another variation of the south slope forest (see map, Fig. 1).

VIII. A slight indentation or concavity of slope, scarcely discernible on the topographic map, and facing south, results in an increase in species, a decrease in chestnut oak (see *VIII* of Fig. 18). The approach to a mixed mesophytic forest is indicated by the presence of tulip tree, cucumber, and red maple in the canopy, the great increase in dogwood, redbud, and sugar maple in the understory, the absence of the heath layer, and the presence of many mesophytic species in the herbaceous layer (Table 7). Again the tension line between climatic and edaphic factors is evident, demonstrating that in only the most extreme habitats (as regards ground water) can the regional mixed mesophytic forest be displaced.

IX. Higher, where all trace of the indentation of slope is lost, the chestnut oak forest prevails. On the higher slopes, from about 2,800 feet to the summit, the oaks are the knarly form assumed in the driest or the shallow soil situations. The aspect is rather barren, the undergrowth sparse, except for occasional bands of *Kalmia* wherever sandstone is exposed.

X. Just under the summit ridge, a massive sandstone stratum forms cliffs 20 to 30 feet in height. At the foot of these cliffs, the chestnut oak forest assumes more of a forest aspect, the trees are taller, straighter and closer together; there is a good leaf litter, and an increase in deciduous shrubs, especially red azalea. Dogwood, too, is abundant. Herbaceous plants are absent, unable to live in the deep accumulation of oak leaves.

The south slope transect ends in the chestnut-chestnut oak forest of a flat-topped portion of River Ridge. The top of the cliffs is fringed by a broad dense belt of *Kalmia* (Fig. 8E). It is only about 200 feet across this

flat-topped summit ridge to the mixed mesophytic forest of the north slope. The variations of the ridge forest are considered in the section on River Ridge.

SOUTH SLOPE RAVINES

South Slope Ravine Transect

The ravine traversed is shorter (hence steeper in its lower course) and much more open (less hemmed in by bordering ridges) than the valley of Joe Day Branch. Since the steeper more open valley faces south-southwest, the pronounced mesophytism displayed emphasizes the climatic character of the mesophytic forest. The south slope ravine, except within a few hundred feet of its mouth, rises steeply with an average gradient of about one foot in

AREA No.→ No. of TREES	SOUTH SLOPE RAVINE										UPPER L.F. COLLIERS CR.			
	I	II	III	IV	V	VI	VII	S III	TOTAL I-VII	%	I	II	III	IV
	94	35	90	81	22	33	17	15	372	%	107	51	20	
<i>Castanea dentata</i> chestnut										18.0	X			
<i>Liriodendron tulipifera</i> tulip tree										15.6	X			
<i>Acer saccharum</i> sugar maple										13.7	X			
<i>Fagus grandifolia</i> beech										10.5	X			
<i>Quercus montana</i> chestnut oak										9.4	X			
<i>Quercus borealis maxima</i> red oak										5.6				
<i>Carya</i> spp. hickory										5.6				
<i>Tsuga canadensis</i> hemlock										5.6				
<i>Acer rubrum</i> red maple										4.3				
<i>Nyssa sylvatica</i> sour gum										2.7				
<i>Magnolia acuminata</i> cucumber tree										2.4	X			
<i>Tilia heterophylla</i> + basswood										1.6	X			
<i>Aesculus octandra</i> buckeye										1.6				
<i>Robinia Pseudo-Acacia</i> black locust										1.1				
<i>Fraxinus biltmoreana</i> + ash. <i>F. americana</i>										.8				
<i>Quercus alba</i> white oak										.5				
<i>Prunus serotina</i> wild black cherry										.3				
<i>Juglans nigra</i> walnut										.3				
<i>Betula allegheniensis</i> birch										.3				
<i>Ostrya virginiana</i> hop hornbeam														

FIG. 19. Percentage composition of canopy of forest communities of ravine on south slope of River Ridge and of the upper Left Fork of Colliers Creek. (SIII refers to III of summit forests of River Ridge.)

three (Fig. 2E). It is open to the south, its slopes facing in a southerly direction (southwest to southeast). Nevertheless, it is clothed throughout with mixed mesophytic forest (Fig. 19 and Table 8). Only on the steepest parts of the slope, some 200 feet beneath the crest (area *VI*) does the forest even resemble the forest of general southerly slopes. Rather, it is similar to the forest of northwesterly slopes, although nowhere as rich and luxuriant, and differs from that forest in the unimportance of buckeye and basswood, two of the dominants of northerly slope forests.

I. In the forest of the lower part of the ravine, hemlock, beech and tulip tree are the most important species, comprising 55 percent of the canopy (as is true of the lowest forest community of Joe Day Branch). Sugar maple is unimportant here, as also in that forest, while chestnut, there unimportant, is the fourth species in the canopy. Rhododendron, although present, is not as abundant as in the lower Joe Day forest. The variety of herbaceous plants exceeds that of the corresponding Joe Day forest, where Rhododendron is in part responsible for the scarcity. (Compare area *I* of Figs. 10 and 19 and Tables 3 and 8.)

II. Hemlock and Rhododendron soon drop out; beech and chestnut are now codominant, forming about 50 percent of the stand, and sugar maple begins to increase. The aspect of the forest in general is typical of the mixed mesophytic forest throughout much of its geographic range, although it lacks some of the luxuriance of the most mesophytic forests of the Cumberlands. The outstanding difference between this mixed mesophytic forest (together with the area just downstream, area *I*) and those of northerly slopes of this region is in the herbaceous layer, which there is very luxuriant and continuous and here is open although it contains most of the species of that forest.

III. The extent of slope occupied by mixed mesophytic forest is decreasing as the ravine becomes less pronounced. The mesophytic species extend only a few hundred feet up-slope on either side. Beyond is the oak-chestnut forest of the southerly slope. Chestnut, sugar maple, tulip tree and beech are now the most important species, comprising 72 percent of the canopy.

IV. At about 2,500 feet the gradient increases; there is no longer any stream; ledges outcrop on the steep slopes. The whole aspect is becoming less mesophytic as the ravine but slightly indents the slope, or rather becomes only a concavity of slope. Beech has disappeared, having reached its altitudinal limit—higher on this warm south slope than on the northerly slopes. Sugar maple, tulip tree, and chestnut continue in about the same proportion as below. The prominence and vigor of sugar maple in the understory suggests its increased importance in the future forest from which chestnut is eliminated by blight. The variety of herbaceous plants decreases, at the same time showing an increase in xero-mesophytic species.

V. Continuing upward, the only suggestion of the ravine below is a slight

concavity of slope facing south-southwest. The slope is littered with sandstone fragments; the aspect is less mesophytic than below, although sugar maple continues the most important species.

VI. The steepest part of the slope is reached not far below the crest of the ridge. This steep south-southwest rocky slope still retains some of the mesophytic species, although the forest here approaches in canopy, the oak-chestnut type. *Pyrularia* and wild grape are abundant, and give a mesophytic aspect to the shrub layer. The sparse herbaceous layer contains a number of typical plants of the mesophytic forest.

VII. The uppermost slopes leading to the crest of River Ridge are less steep. Sugar maple again is important. The forest belongs to the sugar maple-chestnut-tulip tree type. This community merges with the sugar maple summit type (*S III* in Fig. 19) in a saddle of River Ridge.

Upper Left Fork of Colliers Creek

The westerly slopes of the Left Fork of Colliers Creek above the last fork, support mesophytic forests comparable to those traversed in the ravine transect, with sugar maple, tulip tree, and chestnut the most important species (areas *I*, *II*, *III* of Fig. 19). The most mesophytic species—buckeye and basswood—are unimportant; beech is present only on the lower slopes. Sugar maple increases in importance upward, reaching a position of dominance high on the slope. The herbaceous undergrowth is mesophytic and varied, although it contains a number of the less mesophytic species common to most westerly slopes, as *Thalictrum dioicum*, *Geranium maculatum*, *Oxalis grandis*, *Desmodium pauciflorum* and *D. grandiflorum*.

The southerly (left-hand) slopes are oak-chestnut except near the ravine, with chestnut dominant on the steep slope above the head of the ravine (*IV* on map, Fig. 1, and chart, Fig. 19).

COMMUNITIES OF THE CREST OF RIVER RIDGE

River Ridge is typical of the narrower mountain crests of Black Mountain. In places, the main crest of Black Mountain is broader, flatter, and hence more mesophytic. Mountain summit forest communities range from mesophytic forests with sugar maple dominant, through various phases of oak-chestnut forest to dwarf knarly oak scrub (10 to 15 feet in height) on very narrow rocky crests. Locally, small "balds" occur. (See chart, Fig. 20, and Table 9.) On the highest parts of Black Mountain in Harlan County additional forest types are distinguishable.

River Ridge itself is dominantly oak-chestnut forest (Fig. 21). Only locally, as at *1*, *8*, and *10* (on map, Fig. 1) are the forests more mesophytic (forest type *III* of River Ridge, Fig. 20, and *S III* of Fig. 18). Due to the former great importance of chestnut, which has died recently, ridge crest

areas in which this tree was abundant (types I and II of Fig. 20) are now dense tangles of young trees growing vigorously. In some places chestnut oak, in others sugar maple, show indications of replacing chestnut.

Wind-swept parts of the ridge are generally mossy and support a sparse ericaceous shrub growth beneath the open oak canopy. Or a dense heath layer may prevail, with *Vaccinium* and *Azalea* most important on the crest and *Kalmia* on the south slope.

An oak scrub, made up of very dwarf chestnut oak (about 10 to 15 feet in height), dwarf chestnut, and an occasional pitch pine prevails on a few knobs of River Ridge (near 2 and at 11 and 12 on map, Fig. 1). Ericaceous shrubs form a lower layer in the oak scrub (Fig. 8F,a, and Table 9, KB).

Heath balds occupy certain knobs and very narrow parts of the ridge (Fig. 8F,b). The "heath bald" community (at 2 on map, Fig. 1) is made up chiefly of *Kalmia*, *Oxydendrum*, *Vaccinium*, *Gaylussacia*, *Azalea*, *Amelanchier* and *Prunus virginiana* with a ground layer of *Galax*, *Epigaea*, *Lycopodium*, and occasional cushions of *Polytrichum* (Table 9, KB). Although small and not dominated by evergreen heaths, the aspect (Fig. 22) is similar to that of some of the shrubby balds of the Southern Appalachians.

FIG. 20. Percentage composition of canopy of mountain summit types along the crest of River Ridge, and of the crest of Black Mountain near the head of Colliers Creek. This latter group is included for comparison (although outside the area of the map) because of the small number of trees in the River Ridge communities, due to its narrowness. I, at 3, 6 and 9; II, at 4 and 7; III, at 1, 8 and 10. NR is narrow ridge, R, ridge, and S, saddle. Summit types: O-C, is oak-chestnut; Tr, transition; M, mixed mesophytic.

AREA No.→ No. of TREES	RIVER RIDGE			BLACK MT. nr Colliers Cr.			SUMMIT TYPES		
	I	II	III	NR	R	S	O-C	Tr	M
	36	18	15	37	174	50	73	192	65
<i>Castanea dentata</i> chestnut									
<i>Quercus montana</i> chestnut oak									
<i>Acer saccharum</i> sugar maple									
<i>Quercus borealis maxima</i> red oak									
<i>Acer rubrum</i> red maple									
<i>Liriodendron tulipifera</i> tulip tree									
<i>Carya</i> spp. hickory									
<i>Nyssa sylvatica</i> sour gum									
<i>Fraxinus biltmoreana</i> & ash. <i>F. americana</i>									
<i>Quercus alba</i> white oak									
<i>Magnolia acuminata</i> cucumber tree									
<i>Tilia heterophylla</i> basswood									
<i>Aesculus octandra</i> buckeye									
<i>Ostrya virginiana</i> hop hornbeam									

Occasionally the summit is nothing more than a narrow rock ridge, then supporting only a few knarly chestnut oaks growing from crevices, and a scattered rock crevice flora in which *Aquilegia canadensis* and *Sedum ternatum* are conspicuous.

UNDERSTORY TREES	I	II	III	K	B	N	R	S
<i>Acer rubrum</i>							X	X
<i>Acer saccharum</i>		X	X				X	X
<i>Amelanchier canadensis</i>	X			X	X			
<i>Amelanchier</i> sp.				X				
<i>Carpinus caroliniana</i>			X					
<i>Carya</i> sp.						X		
<i>Castanea dentata</i>			X	X			X	X
<i>Cercis canadensis</i>		X						
<i>Cornus florida</i>	X	X	X					
<i>Fraxinus</i> sp.			X				X	
<i>Liriodendron tulipifera</i>						X		
<i>Magnolia acuminata</i>			X					
<i>Ostrya virginiana</i>						X		
<i>Oxydendrum arboreum</i>		X		X	X	X		
<i>Pinus rigida</i>				X				
<i>Prunus serotina</i>		X						
<i>Quercus alba</i>						X		
<i>Quercus borealis maxima</i>		X				X	X	
<i>Quercus montana</i>	X	X	X	X				
<i>Robinia pseudo-acacia</i>						X		
<i>Sassafras variifolium</i>				X		X		
<i>Tilia heterophylla</i>			X				X	
SHRUBS & WOODY CLIMBERS								
<i>Crataegus</i> sp.				X				
<i>Gaylussacia baccata</i>				X				
<i>Hamelis virginiana</i>	X			X		X		
<i>Kalmia latifolia</i>	X			X				
<i>Menispermum canadense</i>			X					
<i>Prunus virginiana</i>				X				
<i>Pyrolaria pubera</i>	X				X	X		
<i>Rhododendron (Azalea), red</i>	X	X		X	X	X		
<i>Rubus</i> sp.	X				X			
<i>Saxifraga oppositifolia</i>	X	X			X			
<i>Vaccinium corymbosum</i>	X	X		X	X	X		
<i>Vaccinium stamineum</i>	X			X				
<i>Vaccinium vacillans</i>	X			X		X		
<i>Vaccinium</i> sp.				X				
<i>Viburnum acerifolium</i>				X	X			
GROUND HEATHS								
<i>Epigaea repens</i>	X			X				
<i>Galax aphylla</i>	X			X				
FERNS & FERN ALLIES								
<i>Adiantum pedatum</i>		X						
<i>Aspidium noveboracense</i>	X					X	X	
<i>Betula virginiana</i>		X	X					
<i>Dicksonia punctilobula</i>						X	X	
<i>Polystichum acrostichoides</i>		X						
<i>Lycopodium complanatum</i>				X				
<i>Lycopodium flabelliforme</i>								
<i>Lycopodium tristachyum</i>				X				
HERBS	I	II	III	K	B	N	R	S
<i>Agrimonia mollis</i>			X					
<i>Asphodelus monica</i>							X	
<i>Andropogon scoparius</i>					X			
<i>Angelica villosa</i>					X			
<i>Antennaria plantaginifolia</i>	X				X			
<i>Aquilegia canadensis</i>					X			
<i>Aralia racemosa</i>							X	
<i>Asclepias physaloides</i>							X	
<i>Aster cordifolius</i>			X					
<i>Astilbe biternata</i>			X					
<i>Caulophyllum thalictroides</i>		X						
<i>Cimicifuga racemosa</i>		X						
<i>Cirsium luteum</i>			X					
<i>Collinsonia canadensis</i>							X	
<i>Conopholis americana</i>							X	
<i>Coreopsis major</i>	X						X	
<i>Cynoglossum virginianum</i>		X						
<i>Cypripedium acaule</i>							X	X
<i>Delphinium tricornis</i>	X	X	X					
<i>Dioscorea villosa</i>							X	
<i>Disporum lanuginosum</i>		X						
<i>Disporum aciculatum</i>			X					
<i>Eupatorium purpureum</i>			X					
<i>Gentiana decora</i>	X	X					X	
<i>Geranium maculatum</i>	X	X					X	X
<i>Helianthus</i> sp.							X	
<i>Hieracium venosum</i>							X	
<i>Hybanthus concolor</i>			X					
<i>Hydrophyllum macrophyllum</i>			X					
<i>Hypoxis hirsuta</i>	X							
<i>Liparis liliifolia</i>							X	
<i>Lysimachia quadrifolia</i>			X				X	
<i>Nedocia virginiana</i>		X						
<i>Monarda</i> sp.							X	
<i>Orchis spectabilis</i>		X	X					
<i>Osmorhiza Claytoni</i>			X					
<i>Pedicularis canadensis</i>	X	X	X				X	
<i>Podophyllum peltatum</i>		X					X	
<i>Polygonatum commutatum</i>			X					
<i>Polymania canadensis</i>			X					
<i>Potentilla canadensis</i>			X					
<i>Potentilla pusilla</i>	X							
<i>Prenanthes serpentina(?)</i>							X	
<i>Ranunculus hispidus</i>							X	X
<i>Sedum ternatum</i>	X	X	X					
<i>Silene stellata</i>		X					X	
<i>Smilacina racemosa</i>							X	
<i>Solidago caesia</i>		X					X	
<i>Stachys cordata</i>							X	
<i>Taenidia integririma</i>			X					
<i>Thalictrum dioicum</i>		X						
<i>Thalictrum</i> sp.		X					X	
<i>Thaspium aureum atropurpureum</i>							X	
<i>Trillium erectum</i>		X						
<i>Trillium grandiflorum</i>	X	X	X				X	X
<i>Trillium undulatum</i>							X	
<i>Uvularia grandiflora</i>	X	X						
<i>Uvularia perfoliata</i>		X					X	

TABLE 9. Undergrowth of communities of the crest of River Ridge and of the crest of Black Mountain near the head of Colliers Creek, Fig. 20. I at 3, 6 and 9; II at 4 and 7; III at 1, 8 and 10; K (knobs with oak scrub) at 11, 12 and near 2; B (balds) at 2.

Wherever the crest is very narrow only fifteen or twenty feet may intervene between the pine-heath or oak-heath of the uppermost south slopes and the mixed mesophytic forest of the northerly slopes (Fig. 8F). The crowns of the trees of the mesophytic forest may project above the ridge crest, the Trilliums and larkspurs come onto the ridge (Fig. 8E, F).

Saddles on River Ridge (as at 1, 8, and 10) are mesophytic, with sugar maple dominant (III of River Ridge, Fig. 20). These forests are a continuation of or modification of the northerly slope forests which in these situations extend up onto the summit.

On the crest of Black Mountain itself, the more mesophytic sugar maple-chestnut and chestnut-maple-red oak forest communities are more extensive than on River Ridge (S and R of chart, Fig. 20). The mesophytic herbaceous



FIG. 21. Chestnut oak forest with Kalmia layer, characteristic of narrow parts of crest of River Ridge. May 8.



FIG. 22. Heath bald and scrub of high knob of River Ridge, at 2. May 4.

layer is here richer than in other ridge-top communities, with *Trillium grandiflorum* conspicuous in the vernal aspect and ferns (*Aspidium noveboracense* and *Dicksonia punctilobula*) conspicuous in summer. Chestnut oak-chestnut forests occupy the narrower parts of the main crest, as they do such spurs as River Ridge (NR of Fig. 20).

SPECIES BEHAVIOR AND INDICATOR SIGNIFICANCE

From the text and charts, the community range and habitat requirements of many species of the area can be ascertained. Certain species, however, because of their community or habitat limitations, are more or less significant in regional studies.

Beech is present in a variety of communities, often not the most mesophytic. Its limitation to lower slopes is not related to fogs, for fog clouds or bands of mist are more prevalent higher, in the sugar maple-basswood-buckeye belt. Although within the area of the map limited to communities below 2,000 or 2,200 feet, it is present in other parts of the Cumberland Mountains at altitudes higher than those attained by the ridges of the area under discussion. At 4,000 feet it is a minor constituent of the forest. It is absent at the intermediate elevations, between about 2,000 and 4,000 feet.

White oak is limited to lower elevations, often occurring with beech and hemlock, or codominant with beech (in other parts of the Cumberlands). It is a constituent of the mixed mesophytic more often than the oak-chestnut forest. White oak, like beech, occasionally occurs at about 4,000 feet.

Chestnut has an exceedingly wide community range; in fact it is absent from only three of the seventy-nine communities illustrated by the charts. Hence as an indicator species it is valueless. It is present in the most mesophytic ravine slope forests, and as a dwarf in the oak scrub of wind-swept crests. Its presence is not indicative of oak-chestnut forest.

Sugar maple is present throughout the entire range of elevation in the area, although it increases in importance upward, often assuming a dominant rôle at about 3,000 feet (Figs. 10, 19). It is not present where the humus layer is duff (mor). It has been shown to be an important species contributing to a decrease in acidity of the forest floor (Alway, Kittredge, and Methley, 1933). Sugar maple and beech seldom attain importance in the same community and never are codominant.

Basswood and buckeye are the most mesophytic species of the mixed mesophytic forest, almost always absent from transitional forest types, and absent or uncommon in the mixed forest of southerly slopes. They never occur except in the mixed mesophytic forest.

Walnut, which has low frequency in the mixed mesophytic forest, nevertheless is present in a number of stands. It is not a constituent of the oak-chestnut. Butternut is less generally present, and equally limited. Wild black cherry occurs more commonly above 2,500 feet.

Chestnut oak, although present in most of the segregates of the mixed mesophytic forest, is never an important species except in the oak-chestnut forest. Scarlet oak is confined to the oak-chestnut or oak-pine variant of it.

Species of the inferior layers show comparable community limitations. Dogwood is a common understory tree in the area, present in a wide range of communities, but not in all, and over the entire range of altitude. It is most abundant in chestnut oak forests of the lower slopes (Fig. 23). It is absent from some of the most xeric communities and usually absent or unimportant in the very mesophytic sugar maple-basswood-buckeye community. On the northwesterly slope of the mountain generally, it decreases in amount at higher elevations, but elsewhere seems to show no consistent variation with altitude. In the occasional abandoned clearings, dogwood reproduces freely, there assuming the dense round crown form.



FIG. 23. Dogwood an important understory tree in chestnut oak forest. Low on ridge between Joe Day Branch and Meeting House Branch. May 6.

The study of the inferior layers was not as complete or detailed as the canopy studies; however, the lists (Tables 1-9) clearly show that many shrub and herbaceous species are limited to particular communities or groups of communities; others are more or less indifferent species. Differences between the lower layers of the mixed mesophytic and oak-chestnut forests are apparent from the lists.

DISCUSSION

Within the limited area of the map (about four square miles) and along the lines of the several transects, a great variety of forest communities is encountered. These differ from one another in canopy dominants and the relative importance of these dominants; in composition of the shrub layer, especially as to presence or dominance of heath shrubs; in the composition and density of the herbaceous layer; and in the nature of the humus layer. All appear to be stable communities, reproducing themselves indefinitely, hence climax in nature.⁶ These communities are not always well-defined or sharply delimited; transitional types are frequent. Between the most mesophytic forests of the valley slopes and the most xerophytic of ridge crests there are all gradations. Gradual impoverishment of the mixed mesophytic forest by elimination one by one of its more mesophytic species, and gradual increase in importance of chestnut (present even in the most mesophytic forest stands) and of chestnut oak take place as soil water diminishes in response to topographic situation. Associated also with the transition to drier and more exposed topographic situations is the change from mull to duff (mor) humus layers, which has resulted in gradual elimination of species least tolerant to acid soils and a duff humus layer.

The community (oak-chestnut) which here occupies the subclimax sites—the drier slopes and ridge crests—is a derivative (association-segregate) of the mixed mesophytic forest, just as are the other association-segregates of more mesophytic sites. The oak-chestnut community is, therefore, an association-segregate and at the same time a subclimax (or preclimax) association⁷ in this region, although a climax association elsewhere. Only more or less arbitrarily may the oak-chestnut be delimited. How and where shall the separation be made?

OAK-CHESTNUT FOREST⁸

What percentage of the canopy must be made up of oaks and chestnut for the forest to be called "oak-chestnut"? If only the superior layer, the forest canopy, is considered, it is impossible to make anything but an arbitrary division. However, there are concrete differences in the lower layers. This again raises the question, much discussed recently, as to whether each layer (synusia) of a several-layered community is a distinct entity or whether the entire stand is the concrete entity (Cain, 1936; Gleason, 1936). The strong inter-relation, inter-dependencies, inter-causal factors between layers of a single stand are apparent in the several series of communities existing in the area under consideration.

⁶ The dying out of chestnut within the past few years (effects of blight first became noticeable in 1932) has of course initiated secondary development. It is still too early to foretell what the outcome will be. As this study is concerned with primary types, standing dead chestnut was counted in determining composition of forest communities.

⁷ Subclimax used as defined by Weaver and Clements (1938), and as used by most workers; it is the equivalent of the physiographic climax of Nichols (1923). According to Clements (1936) this oak-chestnut forest would be called a preclimax, because subclimax is by him limited to a climax-like community (a proclimax) which has resulted from disturbance.

⁸ The oak-chestnut forest is here treated separately because it alone of all the segregates becomes a climatic climax elsewhere.

The late spring leafing of oaks and chestnut is an important factor affecting lower layers of the forest. Light, moisture, and humus decomposition are all involved. The delicate mesophytic herbaceous layer made up of mull plants⁹ cannot exist in a forest dominantly oaks and chestnut. Only by considering the community as a whole with all its layers (synusia) is it possible to separate the oak-chestnut from the mixed mesophytic. The boundary between the mixed mesophytic communities and the oak-chestnut communities is placed where the influence of canopy is reflected in inferior layers. This is not to be thought of as a distinct line. To the east and southeast, the oak-chestnut association-segregate has expanded and occupies extensive climax areas and is hence recognized as one of the climaxes of the deciduous forest (Braun, 1938). But within the area under consideration, this oak-chestnut forest is constantly associated with particular physiographic situations, drier sites, and is here a physiographic climax or subclimax. It is no more a second climax in the area than is every other one of the association-segregates found here. It is not constant in percentage of its dominants but varies from place to place. (Note variability displayed by Joe Day ridge chart, Fig. 5.)

If the oak-chestnut subclimax or physiographic climax forest be considered as the sum of all the more xeric communities in the area of the map (Table 10) it is at once evident that two species are dominant, chestnut and

TABLE 10. COMPOSITION OF OAK-CHESTNUT FOREST

Based on 943 canopy trees in areas of oak-chestnut forest traversed by transects. Arranged on basis of number and presence. Note that certain trees of the mixed mesophytic forest (Table 11) are absent from the oak-chestnut forest: basswood, buckeye, ash, walnut, and butternut. Oxydendrum and Amelanchier, which attain a doubtful canopy position in open areas of oak-chestnut forest, are present in the understory of the mixed mesophytic forest. For detailed composition see charts, Figs. 5, 7, 10, 16, 17, 18, and 20.

	Percent		Percent
<i>Castanea dentata</i> ,		<i>Acer saccharum</i> ,	
chestnut	41.9	sugar maple	1.6
<i>Quercus montana</i> ,		<i>Pinus rigida</i> ,	
chestnut oak	25.9	pitch pine	1.0
<i>Quercus coccinea</i> ,		<i>Quercus velutina</i> ,	
scarlet oak	4.8	black oak8
<i>Quercus alba</i> ,		<i>Pinus echinata</i> ,	
white oak	4.6	shortleaf pine7
<i>Acer rubrum</i> ,		<i>Magnolia acuminata</i> ,	
red maple	2.4	cucumber tree6
<i>Nyssa sylvatica</i>		<i>Robinia pseudoacacia</i> ,	
sour gum	2.2	locust, black locust5
<i>Fagus grandifolia</i>		<i>Prunus serotina</i> ,	
beech	2.8	wild black cherry4
<i>Tsuga canadensis</i>		<i>Betula allegheniensis</i> ,	
hemlock	5.1	birch2
<i>Quercus borealis maxima</i> ,		<i>Magnolia Fraseri</i> ,	
northern red oak	1.7	mountain magnolia1
<i>Liriodendron tulipifera</i> ,		<i>Oxydendrum arboreum</i> ,	
tulip tree	1.1	sourwood1
<i>Carya</i> (3 spp.)		<i>Amelanchier canadensis</i> ,	
hickory	1.3	service berry1

⁹ Refers to plants confined to the mull type of humus layer as defined by Romell and Heiberg (1931) and Lutz (1932).

chestnut oak, which together comprise nearly 70 percent of the total.¹⁰ The remaining 30 percent is here made up of twenty-two species. Of these, only scarlet oak, beech and hemlock ever assume important rôles in any community here assigned to the oak-chestnut subclimax association. All except four (scarlet oak, black oak, pitch pine and yellow pine) are present in the mixed mesophytic forest, as well as in the oak-chestnut forest.

With the slightest diminution of the extreme conditions necessary for its development, the oak-chestnut is replaced by some type of mixed mesophytic forest (see area *VIII* of south slope transect, Fig. 18, and area *XI* of Joe Day ridge transect, Fig. 5).

MIXED MESOPHYTIC FOREST

The mixed mesophytic forest is the regional climax, the climatic climax, represented by a number of association-segregates. It occupies all situations except narrow ridge crests and steep slopes facing in southerly or westerly directions. Ravines of steep gradient on south slopes support mixed mesophytic forest (see Fig. 19). The shallowest concavities on the south slope (see area *VIII* of Fig. 18) resemble mixed mesophytic forest more than they do oak-chestnut forest, all layers being considered. Some westerly slopes support mixed mesophytic forest, others oak-chestnut forest. Transitional types of course occur. The forest of some of the ridge crests sloping north (see Meeting House Branch ridge transect, Fig. 17) is better classified as mixed mesophytic than as oak-chestnut, all layers being considered. [Compare, for example, the Meeting House Branch ridge (sloping north) and the Joe Day ridge (sloping northwest). The forest of the former ridge (up to the steep rise where it merges with the mountain slope, that is, through area *IV*) is 50 percent oaks and chestnut, including 17.5 percent of white oak, a mesophytic species commonly associated in the region with beech or beech and hemlock; about 40 percent of its canopy trees are mesophytes, more if white oak be counted here. The forest of the Joe Day Branch ridge, up to the same elevation (that is, through area *I*) is 68 percent oaks and chestnut, including only 4 percent of white oak; less than 30 percent of its canopy trees are mesophytes; except at its lowest elevations, it is oak-chestnut almost throughout.]

If the assemblage of mesophytic communities encountered in the area of the map be considered as together making up the mixed mesophytic forest—a composite concept—we should picture a forest canopy of about twenty-five species, with no pronounced dominants (see Table 11). Mixed forests without dominant species, that is, forests approaching the composite concept, do occur; such mixed mesophytic forests may be made up entirely of deciduous species, or may contain hemlock. In some of the mixed forests, beech is the

¹⁰ While the communities added together in this summation are not of the same area, and differ greatly from one another in number of trees, it is to be remembered that in all cases the studies were made along transects, hence the community is represented by a band, the length of which is dependent on the extent of the community.

TABLE 11. COMPOSITION OF MIXED MESOPHYTIC FOREST

Based on 2,013 canopy trees in areas of mixed mesophytic forest.¹¹ It will be noted that all of the species of the oak-chestnut forest (Table 10) are represented except scarlet oak, black oak, pitch pine and shortleaf pine, four unimportant species totaling only 7.2 percent of the oak-chestnut forest canopy. Amelanchier and Oxydendrum, attaining a doubtful canopy position in open oak-chestnut forest, are in the understory of the mixed mesophytic forest. Hickory is slightly more important in the mixed mesophytic forest than in the oak-chestnut forest. Nyssa is an indifferent species with high presence and low frequency in both forests. Red maple, too, is an indifferent species, more important in the mixed mesophytic than in the oak-chestnut forest. Chestnut in both forests is important and has a high presence and high frequency. Basswood (especially *Tilia heterophylla*), buckeye (*Aesculus octandra*), ash (*Fraxinus Biltmoreana* and *F. americana*), and walnut and butternut (*Juglans nigra* and *J. cinerea*) are trees of the mixed mesophytic forest only. For detailed composition of association-segregates of the mixed mesophytic forest, see charts, Fig. 7, 10, 15, 16, 17, 19, 20.

	Percent		Percent
<i>Acer saccharum</i> , sugar maple	20.27	<i>Magnolia acuminata</i> , cucumber tree	1.84
<i>Castanea dentata</i> , chestnut	12.67	<i>Nyssa sylvatica</i> , sour gum	1.84
<i>Fagus grandifolia</i> , beech	12.27	<i>Fraxinus Biltmoreana</i> & <i>F. americana</i> , ash	1.09
<i>Tilia heterophylla</i> +, basswood	9.15	<i>Betula allegheniensis</i> , birch	1.04
<i>Liriodendron tulipifera</i> , tulip tree	8.25	<i>Magnolia Fraseri</i> , mountain magnolia65
<i>Tsuga canadensis</i> , hemlock	6.85	<i>Prunus serotina</i> , wild black cherry60
<i>Aesculus octandra</i> , buckeye	6.31	<i>Juglans nigra</i> , walnut40
<i>Quercus borealis maxima</i> , northern red oak	4.67	<i>Robinia pseudoacacia</i> , locust, black locust30
<i>Acer rubrum</i> , red maple	3.43	<i>Juglans cinerea</i> , butternut20
<i>Quercus alba</i> , white oak	2.98	<i>Platanus occidentalis</i> , sycamore10
<i>Quercus montana</i> , chestnut oak	2.33	<i>Ostrya virginiana</i> , hop hornbeam05
<i>Carya</i> , spp., hickory	2.19		

most important species. In the forest as a whole, seven species (sugar maple, chestnut, beech, basswood, tulip tree, hemlock, buckeye), which in one or another segregate are important species, comprise about 75 percent of the canopy trees. The remaining 25 percent is made up of less important species.

¹¹ As the mixed mesophytic forest varies with altitude, all communities in the charts are not included here because of the preponderance of low altitude communities. These calculations are based on what are essentially five belt transects selected so as to include a proportionate representation of all parts (altitudinally) of the mountain slope: (1) Joe Day Branch (I-VII) from about 1,600 to 3,400 feet; (2) south slope ravine (I-VII and S III); (3) right fork of Joe Day Branch below 2,000 feet (not shown on charts), plus upper Left Fork of Collier's Creek above 2,000 feet (two groups of forest communities corresponding in slope exposure), plus summit of Black Mountain, type S (which continues the forest above II and III of Left Fork of Collier's Creek); (4) Staggerweed Hollow (I and II) up to about 2,000 feet (exclusive of lateral slopes), plus Collier's Creek above 2,000 feet to the mountain summit (not shown on map or charts, but in type corresponding to Staggerweed above 2,000 feet); (5) Staggerweed Hollow (III, V, VI), slopes below about 2,000 feet, plus about an equal area of slopes above 2,000 feet (Joe Day Branch ridge, northerly slopes; V, Na and b; VII, N; X, N; and an area above X not on chart). Meeting House Branch is not included; the inclusion of its communities without an equal extent of higher altitude communities would give undue weight to low altitude trees (as beech and hemlock) in the picture of the mixed mesophytic forest as a whole.

Of these, white oak (comprising about 3 percent of the forest as a whole) is an important species in some communities at the lowest elevation in the region. Red oak has a high presence in mixed mesophytic communities but never in this region can be considered as one of the dominants of an association-segregate.¹²

The differences between the mixed mesophytic climax association and the oak-chestnut subclimax association (composite concepts) are apparent in the tables (Tables 10 and 11).

ASSOCIATION-SEGREGATES OF THE MIXED MESOPHYTIC FOREST

The various segregates of the mixed mesophytic forest differ strikingly from one another in canopy composition, generally less so in lower layers (see charts, Figs. 10, 15, 16, 19, and Tables 3, 4, 5, 8). Changes from one to another community of a series are gradual, and evidenced particularly in decreasing importance of some and increasing importance of other species, as shown by the charts. Certain segregates, because of their general occurrence in the Cumberland Mountains as a whole, should be recognized: beech-hemlock; sugar maple-basswood-buckeye; chestnut-sugar maple-tulip tree; beech-chestnut (with ericaceous layer); white oak-beech (with or without hemlock).

The beech-hemlock or hemlock-beech association-segregate always has a large number of species, several of which, as tulip tree, red maple, white oak, and chestnut, may be important. It grades into the mixed forest containing hemlock. *Rhododendron maximum* is in places important in an inferior layer. In such places the humus layer may be duff (mor) and the herbaceous vegetation sparse. This community is sometimes said to be postclimax, as it generally occurs low in ravines. However, both of its dominant species take prominent part in communities transitional to subclimax oak-chestnut, such as beech-chestnut-chestnut oak or hemlock-chestnut-white oak; and either or both are frequently present in typical oak-chestnut forest of this region. Beech is distinctly not a postclimax species in this region; although a usual constituent of ravine slope forests below about 2,000 feet elevation, it is abundant on west and southwest slopes and ascends to higher elevations on these slopes than on northerly slopes (see charts).

The sugar maple-basswood-buckeye association-segregate is one of the best defined and most extensive of all the forest types (Figs. 11, 12). It is found at elevations above 2,000 feet over much of the mountain slopes except where these face in southerly direction or are strongly convex. At its lower altitudinal limits, beech is present; as its upper limits are approached, sugar maple increases in importance, in places assuming a dominant rôle. In some areas, tulip tree is an important constituent. Transitions to the sugar maple-chestnut, or sugar maple-chestnut-tulip tree are also seen. Because of its definite altitudinal relations and widespread occurrence, the sugar maple-

¹² When the mixed mesophytic forest over its whole geographic range is considered, there is some difference in the order of importance of species, beech and white oak assuming greater importance, chestnut less. Additional species are represented elsewhere.

basswood-buckeye association-segregate is, in Clements' terminology (1936), a faciation.¹³ In herbaceous layer, this forest is the most luxuriant of the whole mixed mesophytic forest (Fig. 13). The soil is deep, the humus layer typical mull.

The chestnut-sugar maple-tulip tree is an important segregate above 2,000 feet on southerly and westerly slopes. It is less mesophytic than the sugar maple-basswood-buckeye forest, although both contain many of the same species both in canopy and inferior layers. In some places, chestnut oak is an important species, then indicating a transitional stage between mixed mesophytic and oak-chestnut. The sugar maple-chestnut forest may be considered as a variation.

The beech-chestnut community is a well marked although not extensive association-segregate. It generally occupies west and southwest slopes below 2,000 feet. *Rhododendron* or *Kalmia*, or both, are important shrubs (Fig. 9). The humus layer is intermediate in character, or varies from place to place. Beech and chestnut are the two most important species, although most of the trees of the mixed mesophytic forest except basswood and buckeye are present. The transitional position of this type, between the beech-hemlock forest or the mixed mesophytic forest without hemlock and the oak-chestnut forest is evident. Chestnut oak may be an important species, then emphasizing the transition to the oak-chestnut forest.

The white oak-beech association-segregate is very important at low elevations in the Cumberland Mountains and in the Cumberland Plateau, generally occurring on more or less southerly or westerly exposures (Braun, 1935, pp. 554, 556). In the area of the map, it is seen on the low hills adjacent to the Cumberland River, and is usually more or less disturbed. Hemlock is sometimes an important species (Fig. 15, VI). In drier situations, in a transition to oak-chestnut, white oak, hemlock, and chestnut are important (Fig. 16, W1, W3).

Many of the communities delimited on the charts are not readily referable to any one of the segregates of the mixed mesophytic forest; some are intermediate between recognizable segregates, or are transitional to the oak-chestnut forest. The multiplicity of groupings which exists (demonstrated on the charts), the complex intergradations displayed, all indicate that visible communities are a result of sorting of species of the mixed mesophytic forest, generally in response to slightly different environmental factors and species requirements. The relatively clear-cut communities of the northern part of the deciduous forest do not exist in this central region where there are a larger number of species and where the time available for forest development has been immeasurably longer. The individualistic concept suggested by Gleason (1926) might be applicable here, where communities with rather definite visible expression are the result of sorting under influences which

¹³ The occasional occurrence of a sugar maple-basswood-buckeye-tulip tree community at low elevations elsewhere in the range of the mixed mesophytic forest association (for example, in southern Ohio) makes use of the genetic term, association-segregate, preferable to faciation for this community.

have been in continuous operation for long periods of time. The sum of all these closely related communities is mixed mesophytic forest, and any one may be termed a mixed mesophytic forest.

When viewed as a whole, the mixed mesophytic forest is seen to occupy by far the greater part of the area under consideration. Early in May, when most of the trees of the mixed mesophytic forest are in leaf, and the dominants of the oak-chestnut forest only beginning to leaf, the areal distribution of these two major forest types is clearly seen. Again in late September and early October the two are readily distinguished, for many of the trees of the mesophytic forest have turned red or yellow while the chestnut oak and chestnut are still green.¹⁴ Here the expanse of mixed mesophytic forest is broken only by narrow bands and wedges of oak-chestnut forest extending along narrow ridge crests. The dominance of the mixed mesophytic association is evident.

SUMMARY

The paper is concerned with a study of forest communities occurring in an area of four square miles on Black Mountain in Letcher County, Kentucky. This area is representative of Kentucky southeast of Pine Mountain. Detailed studies were made of nine "transects" along ravines and ridges on the northwesterly and southerly slopes of the mountain and along the mountain crest. Four of these ascend from valley to mountain crest. The composition of forest communities encountered along the transects is shown by charts and tables. These reflect variations due to differences in slope exposure and altitude and emphasize the mixed mesophytic forest as the climatic climax.

Most of the forest communities belong to the mixed mesophytic association of the deciduous forest. Steep southerly and southwesterly slopes, and some of the ridge crests of the northwesterly slopes, support oak-chestnut forest, here a physiographic climax. All ravine slopes, regardless of direction, unless near to ridge crests, support some phase of mixed mesophytic forest. The slightest concavity of south slopes is sufficient to make possible occupancy by a mixed forest which, all layers being considered, is better referred to the mixed mesophytic than to the oak-chestnut association.

The delimitation of oak-chestnut forest cannot be based upon canopy composition alone; lower layers must be considered. The boundary between oak-chestnut and mixed mesophytic communities is placed where the influence of canopy is reflected in inferior layers. In its entirety, the oak-chestnut forest of this area is a forest in which chestnut and chestnut oak (*Quercus montana*) comprise nearly 70 percent of the canopy, the remaining 30 percent or more being made up of twenty or more species. The tables listing

¹⁴ The effect is not greatly changed since the chestnut has died. Nowhere does one see the great areas of dead chestnut so noticeable on slopes of the southern Blue Ridge and Great Smoky Mountains.

understory, shrub, and ground layers demonstrate the differences in specific content between the two associations, as well as the pronounced overlap of species.

The mixed mesophytic forest is the regional climax, here represented by a number of distinct association-segregates and transitional communities. In its entirety it is a forest of some twenty-five canopy species of which seven (totalling 75 percent) are important species in one or another segregate.

The beech-hemlock, sugar maple-basswood-buckeye, chestnut-sugar maple-tulip tree, beech-chestnut (with ericaceous layer), and white oak-beech are the most important association-segregates; undifferentiated mixed forests approaching the composite concept of the mixed mesophytic also occur. The sugar maple-basswood-buckeye forest is the best defined of the forest types. It is found at elevations above 2,000 feet on all northerly and northeasterly slopes. The sum of all these closely related communities represents the mixed mesophytic association of the deciduous forest.

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INTERCEPTION OF RAINFALL BY PRAIRIE GRASSES,
WEEDS, AND CERTAIN CROP PLANTS¹

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INTERCEPTION OF RAINFALL BY PRAIRIE GRASSES, WEEDS, AND CERTAIN CROP PLANTS

INTRODUCTION

Much attention has been given to loss of water through runoff, evaporation from the soil, and by transpiration. Water loss sustained through interception by herbaceous vegetation has received very little consideration.

Studies at forest meteorological stations in Europe, as early as 1855, included comparisons of rainfall in evergreen and deciduous forests with precipitation in the open (Zon, 1927; Horton, 1919). Marloth (1903, 1905), in South Africa found that the amount of moisture deposited in a rain gauge screened by reed-like plants exceeded the amount caught in one unscreened. During normal precipitation the interception gains were 300 percent or more, but during misty weather they ranged from 1,000 to 1,500 percent. Horton (1919) measured interception by trees, crops, and other herbaceous vegetation. He calculated interception losses on a drainage basin near Seneca Falls, New York. The percentage of loss varied with intensity of rainfall from nearly 100 during light showers to an average of 25 for most trees during heavy rains. Interception losses from needle-leaved trees were found to be greater than from broadleaved trees, because of greater storage capacity and evaporation. The total interception losses from cropped areas were much less than from trees because of the short time during which the crops were on the ground.

Phillips (1926, 1928), working in South Africa, found that rain gauges under vegetation registered from 0.0025 to 0.015 inch during foggy or misty weather when no actual rainfall had occurred in the open. Gauges screened with branches of a broadleaved conifer (*Podocarpus thunbergii*) registered from 158 to 181 percent greater precipitation than those in the open, except when the precipitation occurred in the form of normal, heavy showers. In Maryland, de Forest (1923) found, during a growing season of four months, that a gauge screened by imitation reed pieces of tin registered an interception gain of nearly 30 percent over a control gauge. Mitchell (1930) reported that a forest cover in Wisconsin prevented about 20 percent of the total rainfall from reaching the ground. Interception losses were greater in jack pine forest than in hardwood-hemlock forest. In the latter, they were greater during the spring when the trees were in leaf than in the fall when the leaves had been shed. Holch (1931) found that an oak forest in eastern Nebraska intercepted 16.1 percent of the rainfall. A linden forest, because of the denser canopy, intercepted 27.2 percent.

Beall (1934) compared penetration of rainfall through the canopy of a mixed white pine and red pine forest in Canada with that of a mixed hardwood forest, consisting mainly of beech, sugar maple, and yellow birch. In spite of nearly equal density of canopy, interception (40 percent) was greater

in the pine forest than in the hardwood forest, where it was 20 percent. The softwood species afforded a greater number of angles and rounded surfaces than did the hardwoods whose smoother surfaces shed droplets readily. The presence or absence of hardwood foliage was not found to have any marked influence upon the percentage of rainfall reaching the ground. Studies by the United States Forest Service, compiled by Munns and Sims (1936), have been reported in "Forests and Flood Control." Interception during significant rains was found to be from 1 to 37 percent of the total rainfall, depending upon the composition, age, and condition of stand and season of year. Wood (1937) found that the average catch of gauges in a mixed forest of oak, pine, and gum was 87 percent of that in the open. The amount of precipitation reaching the ground in a forest was found to vary with character of the forest, nature of the precipitation, and velocity of wind. The proportion of precipitation penetrating the crown of a chestnut oak did not increase after the leaves fell. McMunn (1936) reported that the foliage of an apple tree shed a considerable amount of rain, thus building up a large volume of water at the periphery of the tree.

A study of interception by the vegetative canopy of crop plants has been reported by Haynes (1937). Interception varied from 6.9 to 35.8 percent of the total precipitation, increasing directly with increase of vegetative cover. Part of the rainfall reaching the ground under corn, alfalfa, and soybeans was conducted down the stems. In other crops the amount reaching the soil in this manner was not significant. Kittredge (1938) has calculated the sum of water losses caused by transpiration and interception by the vegetation, evaporation from the soil, and seepage into rock strata. The most important of these are the losses influenced by vegetation. Water losses in two types of grassland were as large as those in certain forest regions.

Interception of rainfall by vegetation is important in the control of surface runoff and soil erosion. There is an inverse relation between interception losses and the water supply of the soil. It has been shown that, under certain conditions, absorption of water by the aerial portions of plants is possible, although favorable conditions for absorption by mesophytes probably occur only rarely in nature (Maximov, 1929; Williams, 1932; Purer, 1936). Interception gains have been recorded under vegetation when the precipitation occurred in the form of misty rains (Marloth, 1903, 1905; Phillips, 1926, 1928). It is a matter of common observation that the ground beneath a tree may be moistened by drip from branches and leaves during a fog while beyond the crown the soil is dry.

The present investigation was undertaken in order to develop and test the suitability of various methods for studying interception by native prairie vegetation, certain crop plants, and weeds and to determine the magnitude of the water losses sustained. Preliminary work was done during 1936. This was followed by extensive experiments throughout the growing seasons of 1937 and 1938. All the plant materials were secured within a radius of

twenty miles of Lincoln, Nebraska. The season of 1937 was one of severe drought. This made necessary the development of a method by which water could be sprinkled upon the plants in a manner resembling natural rainfall (Clark, 1937). These experiments were continued during 1938 and extended to include interception of natural rainfall by certain prairie grasses and field crops.

The writer wishes to express sincere appreciation to Dr. J. E. Weaver for outlining the problem and for efficient direction throughout the investigation.

METHODS

Since rainfall interception was measured during a long period of drought, it was necessary to devise a method of applying water to the plants in a manner closely resembling natural rainfall. After a number of trials, two methods were developed and used in the collection of data, one in the field trials and the other in experiments in the greenhouse and laboratory. While these experiments do not simulate all the conditions existing during a shower or rainstorm, yet the results obtained closely followed those secured from natural rainfall.

For experiments in the field, special pans were constructed to catch some of the water which was not intercepted by the plants. The pans were 100 cm. long, 4 cm. wide, and 5 cm. deep, and were made of 24-gauge galvanized iron, soldered at the corners so as to be watertight. Five pans thus had a surface area of one-fifth of a square meter. Permanent cross wires at intervals of an inch near the top of each pan and a removable strip of wire mesh in the bottom made it possible to support cut stems of plants in their natural position. By means of tall stakes, a square meter quadrat was located in the vegetation to be studied. Five of the interceptometer pans were placed on the surface of the soil beneath the plants, care being taken to space the pans uniformly with minimum disturbance of the vegetation. Where crops, such as wheat or oats, were drilled they were placed across the drill rows. Whenever necessary to permit proper placing of the pans, plants were cut off at the soil surface and inserted in them in the same position that they originally occupied. After some experience it was possible to place the pans so that the foliage cover closely resembled that of adjacent undisturbed areas. A quadrat in big bluestem prairie with these interceptometers in position is shown in Figure 1. They are partly withdrawn to show something of their construction in Figure 2.

Water was applied to the plants from two-liter glass bottles equipped with fine sprinkler tops and glass tubing so that it issued from the sprinklers in steady streams but struck the plants in the form of drops. A total volume of water equivalent to 1 or 2 inches of rainfall upon the area or some fraction of an inch per hour or half hour was calculated and kept on hand. It was then sprinkled upon the plants uniformly during the predetermined time in-



FIG. 1. Interceptometers in position in a square meter of big bluestem prairie.



FIG. 2. Interceptometers partly withdrawn to show something of their construction.

terval. The amount of water caught in the five pans equalled one-fifth of the water penetrating the foliage cover and reaching the ground. From the result obtained it was possible to calculate the amount of water intercepted by the plants and to express it as a percentage of the total amount applied. Experiments were performed in both lowland and upland prairies, with field crops, and with a considerable variety of weedy plants.

Evaporation rates were measured by Livingston's spherical, white, porous-cup atmometer, mounted on a small graduate so that readings could be made directly. The apparatus, placed near the experimental area, was adjusted to bring the atmometer to a level with the tops of the plants. Before and after each trial the air temperature and relative humidity were recorded. Conditions of sky and wind movement were also noted.

Since it was impossible to use the field procedure on mat-forming or low-growing plants, a method was devised to be used in the laboratory or greenhouse. Field plants were cut off at the surface of the soil by means of a sharp spade, wrapped in moist cloth or paper, and placed in containers for transportation to the laboratory. They were then placed in their natural position upon a quarter-inch mesh wire screen so as to give a typical foliage cover over an area of a square foot, a square meter, or a square yard. The screen was suspended from a frame over a large funnel, 3 feet in diameter, or a pan, 3 feet square, by means of which the water penetrating the plant cover was caught. The plants were then sprinkled with a known amount of water or until it was certain that the maximum interception capacity had been reached. Interception was expressed as a percentage of the total amount applied or as a gain in weight of the plants. To correct for water held by the screen and funnel, they were sprinkled before the plants were placed in position. Air temperature, relative humidity, and evaporation were recorded as in the field experiments. The effect of wind movement was obtained by the use of a 16-inch electric fan. The apparatus, set up outside the laboratory, is shown in Figure 3. In addition to living plants, an artificial straw mulch and mats of dead, dry grasses were used to determine their interception capacity.

By substituting a wire-mesh basket of one square-foot area for the screen, it was found that the interception capacity of plants with erect stems could also be studied by this method. Accordingly, prairie grasses and various broadleaved species from square-foot areas were brought into the laboratory and treated in the manner described for the mat-formers. Cross wires in the basket made it possible to keep the plants in their normal position.

Interception of rainfall by prairie grasses and crop plants under natural conditions was also measured. The interceptometer pans were fitted at one end with outlet spouts which were connected to half-gallon reservoir bottles by means of rubber tubing. In order to equalize air pressure, a piece of bent copper tubing was inserted through the cork stopper. The bottles were set in a trench, dug along one side of the quadrat but 8 inches from its edge and



FIG. 3. Apparatus for measuring interception by mat-forming plants and densely aggregated grasses.

at a level which permitted an easy flow of water from the pans into the bottles. Rainfall records were obtained from rain gauges placed in open areas in the immediate vicinity of the quadrats. The gauges were read and the water in the bottles measured after each shower or period of rain. Five lots of interceptometer pans and reservoirs were placed in fields of planted crops and in two prairies.

RESULTS

INTERCEPTION BY PRAIRIE GRASSES

Numerous experiments were performed with prairie grasses of lowland areas. Big bluestem (*Andropogon furcatus* Muhl.) grows typically as a sod former, with individual stems about 1 cm. apart. There is much unoccupied soil, the average basal cover being about 13 percent. Nevertheless, the foliage cover in dense stands is usually 100 percent, due to the large number of widely spreading leaves. At the time of the first experiments, late in June, the leaves averaged 22 inches in height. On August 25, the experiments were repeated. The general foliage level averaged 36 inches in height but flower stalks reached a height of 60 inches and the plants were in bloom. A few stalks of other grasses of similar ecological habit were present in the quadrats but forbs were almost absent.

Interception varied inversely with the amount of rainfall, from 84 percent with one-eighth inch in 30 minutes to 47 percent with 1 inch in an hour (Table 1). Even with a rainfall intensity of 2 inches per hour, interception was 51 percent. Just as the foliage cover of two adjacent quadrats was never exactly alike, so, too, the interception from equal amounts of rainfall varied somewhat. Condition of sky and wind movement strongly influenced interception through their effect upon evaporation of moisture from the plant surfaces. The amount of water entering the interceptometers when cut plants were placed in the pans did not differ consistently from the amount obtained when the stems were placed outside. This is taken to indicate that the amount of water running down the stems was not large.

TABLE 1. PERCENTAGE INTERCEPTION BY A SQUARE METER OF BIG BLUESTEM OF LOWLAND PRAIRIE

Date	APPLICATION		Sky	Wind	Temp. Deg. F.	Humidity percent	Evap. cc.	Percent
	Inches	Minutes						
1937								
June 23.....	0.25	30	Clear	Strong	101	27	—	81 ¹
"	0.5	"	"	"	102	26	2.3	66 ¹
June 25.....	0.125	"	Partly cloudy	"	88	64	0.8	65 ¹
"	0.25	"	Cloudy	"	82	76	0.8	57 ¹
June 28.....	0.25	"	"	Moderate	76	70	0.3	61 ¹
"	0.25	"	"	"	75	66	0.4	69 ²
June 29.....	0.25	"	Clear	"	79	47	1.6	69 ¹
"	0.25	"	"	"	78	43	1.6	69 ²
June 30.....	0.125	"	Partly cloudy	Light	89	35	1.2	67 ¹
"	0.125	"	"	"	94	27	1.2	72
July 2.....	0.5	"	Clear	"	89	38	0.8	57 ¹
"	0.5	"	"	"	92	29	1.2	61
Aug. 18.....	1.0	60	Partly cloudy	Moderate	88	61	2.3	47 ¹
"	0.5	30	"	"	94	46	1.6	58 ¹
"	0.25	"	"	"	94	44	2.3	68 ¹
Aug. 25.....	0.125	"	"	Light	86	57	1.6	81 ¹
"	0.125	"	"	"	92	48	1.6	84 ²
1938								
July 20.....	2.0	60	Partly cloudy	Moderate	81	41	—	51 ¹

¹Plants cut where necessary and placed in pans.

²Plants cut but placed outside pans.

Big bluestem areas on upland were studied on July 23 and 30. The plants ranged in height from 15 to 20 inches and flower stalks were just appearing. Very few plants of other species occurred. Interception with one-half inch of rainfall in 30 minutes varied from 50 percent to 63 percent due to differences in density of stand and in the environmental factors affecting evaporation (Table 2). In all of the trials, cut plants were placed in the pans in order to catch water running down the stems.

TABLE 2. PERCENTAGE INTERCEPTION BY A SQUARE METER OF BIG BLUESTEM OF UPLAND PRAIRIE

Date	APPLICATION		Sky	Wind	Temp. Deg. F.	Humidity percent	Evap. cc.	Percent
	Inches	Minutes						
July 23.....	0.5	30	Clear	Strong	97	26	2.3	50
" 30.....	"	"	Partly cloudy	Moderate	85	67	0.8	56
"	"	"	"	Light	88	61	1.6	63
"	"	"	Mostly clear	"	89	59	1.6	51

Interception was also studied, during late July, in an area dominated by big bluestem, but in which were also represented needle grass (*Stipa spartea* Trin.), side-oats grama (*Bouteloua curtipendula* (Michx.) Torr.), and prairie dropseed (*Sporobolus heterolepis* A. Gray). Isolated plants of several characteristic forbs also occurred. The vegetation ranged in height from 18 to 24 inches and the foliage cover was dense and uniform. Interception varied from 57 percent with one-eighth inch in 30 minutes to 43 percent with 1 inch in 60 minutes (Table 3). Under favorable conditions interception with a quarter-inch of rain in a half hour was almost as great as that with one-eighth inch. In each experiment, plants were cut whenever necessary and were placed in the pans.

TABLE 3. PERCENTAGE INTERCEPTION BY A SQUARE METER OF BIG BLUESTEM WITH OTHER GRASSES AND FORBS

Date	APPLICATION		Sky	Wind	Temp. Deg. F.	Humidity percent	Evap. cc.	Percent
	Inches	Minutes						
July 22.....	0.25	30	Clear	Strong	97	33	2.3	54
" 23.....	0.25	"	"	"	97	26	4.0	56
" 29.....	0.25	"	Partly cloudy	Moderate	90	47	1.6	51
"	1.0	60	"	"	92	45	3.1	43
"	0.125	30	"	"	88	49	0.8	57

Needle grass, growing on a gravel knoll in typical, open bunch habit, was studied on July 15. In the quadrats of almost pure needle grass, the leaves had an average height of 15 inches. The flower stalks were 36 inches high and had already shed their fruits. Interception with one-eighth inch of rain in 30 minutes was 59 percent. When one fourth of an inch was applied during a similar period, one-half of the rainfall was intercepted (Table 4).

Interception by prairie dropseed was studied during late July. The open bunch habit was fairly typical of this species considering the drought conditions, but the foliage cover was not as great as during years of normal rain-

fall. The plants were about 12 inches in height but without flower stalks. The inverse relation between intensity of rainfall and the percentage of interception is clearly shown in Table 4. The importance of wind movement is also apparent, increased wind movement increasing the total amount of interception by accelerating evaporation.

TABLE 4. PERCENTAGE INTERCEPTION BY A SQUARE METER OF VARIOUS GRASSES

Date	APPLICATION		Sky	Wind	Temp. Deg. F.	Humidity percent	Evap. cc.	Percent
	Inches	Minutes						
Needle Grass								
July 15.....	0.25	30	Mostly clear	Light	91	51	1.6	49 ¹
”	0.25	”	”	”	94	44	1.6	50 ²
”	0.125	”	”	”	94	39	2.3	59 ¹
Prairie Dropseed								
July 22.....	0.25	30	Clear	Strong	97	28	3.1	54 ¹
”	0.25	”	”	”	97	30	3.9	60 ²
July 28.....	0.125	”	Mostly clear	Moderate	88	46	1.6	53 ¹
”	0.25	”	Clear	”	94	34	3.1	50 ¹
”	1.0	60	”	”	94	32	5.5	29 ¹
Western Wheat Grass								
July 13.....	0.25	30	Cloudy	Strong	86	63	1.2	46 ¹
”	0.25	”	”	”	88	61	1.6	50 ²
Nodding Wild Rye								
July 14.....	0.25	30	Partly cloudy	Moderate	89	55	0.8	62 ¹
”	0.25	”	”	”	85	65	0.8	61 ²

¹Plants cut where necessary and placed in interceptometer pans.

²Plants cut but not placed in pans.

Western wheat grass (*Agropyron smithii* Rydb.), which has greatly increased its area in the middle west during the drought years, was studied on July 13. The plants occurred in a pure stand and averaged 30 inches in height. The spikes were nearly ripe but most of the leaves were still green. Interception with one-fourth inch of rain in 30 minutes was 46 percent when the cut plants were placed in the pans, and 50 percent when they were placed outside the interceptometers (Table 4).

A pure stand of nodding wild rye (*Elymus canadensis* L.) was studied on July 14. The stems were widely spaced in an almost continuous sod, but the percentage of basal cover was low. The plants were about 40 inches in height, headed, and in full bloom. The upper leaves were still green but the lower parts of the stems were bare, which is characteristic of this species. With rainfall of one-fourth inch in 30 minutes, interception was 62 percent

in one trial and 61 percent in another, indicating that no significant amount of water passed down the stems (Table 4).

Experiments with slough grass (*Spartina pectinata* Link.) were performed during July in several typical lowland sites. The foliage cover was nearly 100 percent but the basal cover was very sparse, since the stems were widely spaced. The plants varied in height from 40 to 45 inches and were not in bloom until August 6, when the flower stalks reached an average height of 52 inches. Although the basal leaves were dead, the foliage cover was dense.

That interception is inversely proportional to intensity of rainfall was again shown. On July 8 and 9, during similar periods of time, interception, with one-eighth inch of rain averaged 72.5 percent, with one-fourth inch 68.5 percent, and with one-half inch 55.5 percent (Table 5). On July 21, with conditions less favorable to evaporation, interception with one-fourth inch of rain averaged 77 percent, reflecting a noticeable difference in density of foliage cover. On August 6, when 2 inches of rain were applied during an hour, interception was 74 percent because of conditions which were especially favorable to evaporation. The stand was so dense, moreover, that when the plants became loaded with water, they lodged badly in the strong wind. The results on July 21 show that the amount of water running down the stems was small.

TABLE 5. PERCENTAGE INTERCEPTION BY A SQUARE METER OF SLOUGH GRASS

Date	APPLICATION		Sky	Wind	Temp. Deg. F.	Humidity percent	Evap. cc.	Percent
	Inches	Minutes						
1937								
July 8.....	0.5	30	Partly cloudy	Moderate	85	50	1.6	53 ¹
"	0.5	"	"	"	87	39	1.6	58
"	0.25	"	"	"	90	39	2.3	69
"	0.25	"	"	"	90	42	2.3	68 ¹
July 9.....	0.125	"	"	"	93	40	2.3	70 ¹
"	0.125	"	"	"	94	34	2.4	75
July 21.....	0.25	"	"	Light	91	44	1.6	73 ¹
"	0.25	"	"	"	92	38	1.6	81 ²
1938								
Aug. 6.....	2.0	60	Clear	Strong	83	57	4.0	74 ¹

¹ Plants cut where necessary and placed in pans.

² Plants cut but placed outside pans.

INTERCEPTION BY VARIOUS PRAIRIE FORBS AND WEEDS

The saw-tooth sunflower (*Helianthus grosseserratus* Martens) often forms dense societies in the rich, moist soil of ravines in prairie. During July plants were found ranging in height from 55 to 67 inches, but they were not yet in bloom. The lower portions of the stems were entirely defoliated to a

height of 2 feet or more but the living, green leaves formed a thick layer of foliage. The cover was opened up to a slight extent by the wilting of some of the leaves on the plants which were cut off.

Interception with one-eighth inch of rainfall was 52 percent in one experiment and 69 in another, the difference being due to variability in density of cover. Interception with one-fourth inch was 68 percent when cut plants were placed inside the interceptometers and 36 percent when placed outside. This could be interpreted as indicating that a considerable amount of water entered the interceptometers by running down the stems, but differences in cover must also be taken into account. When the rainfall intensity was increased to one-half inch per half hour, interception decreased to 23 percent, showing that with this species, as with grasses, it was inversely proportional to the intensity of rainfall. The leaf surfaces of this sunflower became wetted uniformly, scarcely any drops being formed. Water ran freely from the tips of the leaves and less readily from the leaf bases.

A perennial smartweed, *Persicaria muhlenbergii* (S. Wats.) Small, also forms dense, nearly pure societies along ravines in the prairie. The plants were nearly 4 feet in height late in July and presented an almost complete foliage cover. This was reduced slightly by wilting of some leaves on the severed plants. They became wetted quickly and uniformly with very few drops forming on the leaves or stems. Interception with one-fourth inch of rain in 30 minutes was 53 percent.

Solidago altissima L., the tall goldenrod, is another common and conspicuous species forming societies in prairies on low ground. On July 20, the plants were over 50 inches tall, but inflorescences had not yet developed. Although the lower parts of the stems were devoid of leaves, the foliage cover was dense because of the large number of green leaves on the upper parts of the stems. Under moderate conditions of temperature and evaporation, and with an application of one-fourth inch of rain in 30 minutes, interception was 46 percent.

Aster salicifolius Lam., the willow-leaved aster, occurs abundantly in lowlands or in ravines where the soil is kept moist by runoff water from adjacent slopes. The plants had reached a height of 52 inches but were not yet in bloom. Some of the cut plants wilted slightly. All became wetted uniformly on the upper surfaces of the leaves and some drops also formed on the lower surfaces. Interception with rainfall of one-fourth inch in 30 minutes was 58 percent.

A characteristic upland forb which has greatly extended its area during the recent years of drought is the many-flowered aster (*Aster multiflorus* Ait.). An almost pure stand of these plants was 24 inches in height on July 26, when the amount of interception was determined. The sky was clear and there was little wind movement. Air temperature was moderate but relative humidity was fairly high. Consequently, evaporation was relatively low.

Under applications of one-fourth inch, one-half inch, and one inch of rain in half-hour periods interception was 52, 37, and 23 percent, respectively. Thus again, the close relationship between rainfall intensity and interception was shown.

The smooth goldenrod (*Solidago glaberrima* Martens) also increased considerably during the drought, especially on upland prairie. Dense, nearly pure stands were 25 inches high, and the plants were beginning to bloom on July 28. Air temperature was moderate and humidity high, resulting in a low rate of evaporation. The sky was mostly cloudy and wind movement varied from moderate to light. During half-hour periods interception was 22 percent with one inch of rain, 30 percent with one-half inch, and 55 percent when one-fourth inch was applied. The plants lodged somewhat under the heaviest application. Neither the goldenrod nor the many-flowered aster wilted during the progress of the experiments. This was in contrast to the behavior of the lowland forbs. The results of experiments with these six forbs are summarized in Table 6.

Interception by one-half square meter of smooth sumac (*Rhus glabra* L.), growing along a ravine in upland prairie, was determined on July 23. The foliage cover was quite open due to the fact that only the upper parts of the stems of this intolerant species bore leaves and that there were only four stems in the quadrat. The sky was clear, a strong wind was blowing, and air temperature and humidity favored rapid evaporation. Although the leaves did not become wetted readily, interception with rainfall of one-half inch in 30 minutes was 38 percent.

The cultivated sunflower (*Helianthus annuus* L.), growing in the rich moist soil of a ravine, had attained by July 12 a height varying from 37 to 65 inches. Flowers had not yet developed. The stand was pure and dense but some of the leaves had been badly damaged by grasshoppers and the foliage cover was further reduced by wilting of a few leaves on the cut stems. Interception, under similar conditions, varied from 34 percent with a rain of one-half inch in 30 minutes to 69 percent with one-eighth inch. Interception with one-fourth inch of rain was 55 percent when the cut plants were placed in the interceptometers and 61 percent when they were placed outside the pans. It is thought that these results do not represent the maximum interception capacity of this species because of the partial reduction in foliage cover.

Amaranthus retroflexus L., the rough pigweed, was growing in a pure, dense stand in a ravine where native vegetation had been covered with eroded soil. It had attained a height of 36 inches on June 17. When one-fourth inch of water was applied in 30 minutes, interception was 71 percent. This wastage of water by interception is a reaction of weeds that is often overlooked, although their value in resisting soil erosion must also be recognized (Kramer and Weaver, 1936).

The saltbush (*Atriplex argentea* Nutt.) is a characteristic plant of the salt flats in the vicinity of Lincoln. On August 17, the plants were 18 inches or more in height and in full bloom. A dense, nearly pure stand of this species intercepted half of the rainfall applied at the rate of one-half inch in 30 minutes.

TABLE 6. PERCENTAGE INTERCEPTION BY A SQUARE METER OF VARIOUS PRAIRIE FORBS

Date	APPLICATION		Sky	Wind	Temp. Deg. F.	Humidity percent	Evap. cc.	Percent
	Inches	Minutes						
Saw-tooth Sunflower								
1937								
July 16.....	0.125	30	Clear	Moderate	86	48	1.6	52 ¹
"	0.25	"	"	"	85	42	1.6	68 ¹
"	0.25	"	"	"	86	39	0.8	36 ²
"	0.5	"	"	"	85	51	0.8	23 ¹
July 21.....	0.125	"	Partly cloudy	Light	86	58	1.6	69 ¹
Smartweed								
July 20.....	0.25	30	Partly cloudy	Light	78	71	0.8	53 ¹
Tall Goldenrod								
July 20.....	0.25	30	Partly cloudy	Light	82	62	0.8	46 ¹
Willow-leaved Aster								
July 20.....	0.25	30	Partly cloudy	Light	86	54	0.8	58 ¹
Many-flowered Aster								
1938								
July 26.....	0.25	30	Clear	Light	90	49	0.8	52 ¹
"	0.5	"	"	"	84	61	0.8	37 ¹
"	1.0	"	"	"	81	65	0.8	23 ¹
Smooth Goldenrod								
July 28.....	0.25	30	Mostly cloudy	Moderate	85	56	1.6	55 ¹
"	0.5	"	"	"	81	65	0.8	30 ¹
"	1.0	"	"	Light	79	70	0.8	22 ¹

¹ Plants cut where necessary and placed in pans.

² Plants cut but placed outside pans.

Kochia scoparia (L.) Schrad., the burning bush, has escaped from cultivation and is commonly found in waste places, where it often forms pure stands. When the plants were about 30 inches tall, on August 17, one-half inch of water was applied in a half hour. Although the foliage did not become wetted readily, under the average summer conditions, interception was 44 percent. Interception by this and the preceding weeds is summarized in Table 7.

TABLE 7. PERCENTAGE INTERCEPTION BY A SQUARE METER OF VARIOUS COMMON WEEDS

Date	APPLICATION		Sky	Wind	Temp. Deg. F.	Humidity percent	Evap. cc.	Percent
	Inches	Minutes						
Cultivated Sunflower								
July 12.....	0.125	30	Partly cloudy	Light	91	59	—	69
"	0.25	"	"	"	91	59	1.2	61 ²
"	0.25	"	"	"	92	57	1.2	55 ¹
July 21.....	0.5	"	"	"	90	42	1.6	34
Rough Pigweed								
July 17.....	0.25	30	Clear	Moderate	—	—	—	71
Saltbush								
Aug. 17.....	0.5	30	Partly cloudy	Moderate	88	64	1.6	50
Burning Bush								
Aug. 17.....	0.5	30	Partly cloudy	Moderate	98	36	2.3	44 ^{**}

¹ Plants cut where necessary and placed in pans.² Plants cut but placed outside pans.

INTERCEPTION BY PLANTED CROPS

The amounts of water intercepted by several crop plants were also ascertained. These included winter wheat (*Triticum aestivum* L.), oats (*Avena sativa* L.), and sweet clover (*Melilotus alba* Desv.).

Lowland winter wheat was about 40 inches high on June 18 and fully headed, although the plants were still green. Similar development was attained by June 20 of the second season, except the lower leaves were entirely dry. The plants were badly affected by rust and were lodged in some places. During all of the experiments, conditions were favorable to evaporation. With rainfall of one-eighth inch in 30 minutes, interception in three trials was 59, 67, and 80 percent, respectively. These differences were largely due to the usual variations in density of stand. With one-fourth inch of rain, interception varied from 51 to 68 percent. When one-half inch of water was applied 53 percent was intercepted. Even with a rain of 2 inches in an hour, interception was 56 and 61 percent. The plants lodged, on account of the wind and the heavy load of water, in the manner commonly observed in badly rusted grain.

The oats were 30 inches high, fully headed but still green, except the lower leaves, when the experiments were performed late in June. The stand was dense and although the plants had been lodged by a heavy rainstorm they had again nearly attained their former erect position. With considerable variation in environmental conditions, interception decreased progressively

from 73 percent, under rainfall of one-eighth inch in an hour, to 43 percent when an inch of water was applied in a similar period. When the rainfall intensity was increased to 2 inches per hour, interception remained the same, reflecting differences in density of stand. The plants lodged as under natural rainfall, when the larger amounts of water were applied.

Plants in the field of sweet clover were nearly 4 feet tall and in full bloom in late June and early July. Because of conditions unusually favorable to evaporation, interception with one-eighth inch and one-fourth inch of rain in an hour was 94 and 92 percent, respectively. With light wind movement, interception decreased to 57 percent when one-half inch of water was applied. With the application of 1 and 2 inches, evaporation was still lower and interception was 47 and 44 percent. Thus, it appears from the results with wheat, oats, and sweet clover that 2 inches of rain so greatly exceed the interception capacity of the plants that the amount of water held is not materially different from that intercepted when 1 inch falls during the same period. Results with planted crops are shown in Table 8.

INTERCEPTION BY MAT-FORMING WEEDS

Interception of rainfall by a square yard or a square foot of mat-forming weeds was determined in the laboratory. The puncture vine (*Tribulus terrestris* L.) was used when it was in full bloom and in fruit. Interception with one-half inch of water in 30 minutes varied from 9 to 15 percent. This variation was due to differences in density of the mats. With rainfall of one-fourth inch and one-eighth inch, interception was 30 and 44 percent, respectively. With the highest intensity of rainfall, the effect of wind movement, produced by an electric fan, was overshadowed by differences in density of the foliage.

Convolvulus arvensis L., the field bindweed, was obtained from a typical, dense, pure growth. Interception increased progressively with decreasing rainfall from 13 percent with one-half inch to 50 percent with one-eighth inch in 30 minutes. The influence of wind movement is well shown by an increase from 13 percent to 18 percent interception with one-half inch of rain (Table 9). Thus, it may be seen that a dense growth of bindweed, in addition to using soil moisture and nutrients and sometimes choking out crop plants, is detrimental in preventing a large amount of water from reaching the soil.

Typical mats of purslane (*Portulaca oleracea* L.) and the prostrate pigweed (*Amaranthus blitoides* S. Wats.) gave similar results with equal amounts of rainfall. In both species interception was 20 percent with a rain of one-half inch in 30 minutes and 17 with one inch in 60 minutes. Differences in air movement produced by low and high speeds of the fan did not

TABLE 8. PERCENTAGE INTERCEPTION BY A SQUARE METER OF PLANTED CROPS

Date	APPLICATION		Sky	Wind	Temp. Deg. F.	Humidity percent	Evap. cc.	Percent
	Inches	Minutes						
Winter Wheat								
1937								
June 18.....	0.125	30	Clear	Strong	—	—	—	59
"	0.125	"	"	"	—	—	—	67 ¹
June 19.....	0.125	"	"	"	93	43	—	80
June 18.....	0.25	"	"	"	—	—	—	51
June 19.....	0.25	"	"	"	89	—	—	68
"	0.5	"	"	Light	84	60	—	53
1938								
June 20.....	2.0	60	Partly cloudy	Moderate	88	73	4	61 ¹
"	2.0	"	"	"	89	48	3	56 ¹
Oats								
June 24.....	0.125	60	Partly cloudy	Strong	90	74	4	73 ¹
June 27.....	0.25	"	Clear	Moderate	71	57	3	57 ¹
"	0.5	"	"	"	74	58	2.4	58 ¹
"	1.0	"	"	"	75	58	3	43 ¹
June 28.....	2.0	"	Partly cloudy	"	73	63	2.4	43 ¹
Sweet Clover								
June 30.....	0.125	60	Mostly clear	Strong	94	39	6.3	94 ¹
"	0.25	"	"	"	97	37	8	92 ¹
July 1.....	0.5	"	"	Light	97	46	3	57 ¹
July 6.....	1.0	"	Partly cloudy	Very light	87	50	1.6	47 ¹
July 7.....	2.0	"	"	Moderate	83	53	3	44 ¹

¹ Plants cut where necessary and placed in pans.

cause a significant difference in interception. Water was held on the pigweed mostly as a uniform film and the plants dried very quickly. The purslane held the water in the form of numerous drops. The leaves did not dry as readily and the plants resisted wilting longer after sprinkling.

Unusually large mats of *Polygonum aviculare* L., knotweed or knot-grass, were obtained on the trampled soil of a playground. In all trials a wind velocity of 12 miles per hour was used and the application period was 30 minutes. The leaf surfaces did not become wetted readily or uniformly, the water being held chiefly as drops on the surfaces of the leaves and in the angles between the leaves and the stem. Interception increased from 13 percent with a half inch of rain to 40 percent with one-eighth of an inch. Results with these mat-forming plants are summarized in Table 9.

TABLE 9. PERCENTAGE INTERCEPTION BY MAT-FORMING WEEDS

Date	APPLICATION		Area	Wind	Temp. Deg. F.	Humidity percent	Evap. cc.	Percent
	Inches	Minutes						
Puncture Vine								
Aug. 3.....	0.5	30	1 sq. yd.	None	—	—	—	15
"	0.5	"	"	"	—	—	—	12
"	0.5	"	1 sq. ft.	"	—	—	—	9
Aug. 4.....	0.5	"	1 sq. yd.	"	86	57	0.8	10
"	0.5	"	"	10 m.p.h.	88	52	3	13
"	0.25	"	"	"	90	44	3	30
"	0.125	"	"	"	90	44	3	44
Bindweed								
Aug. 5.....	0.5	30	1 sq. yd.	None	88	49	1.6	13
"	0.5	"	"	10 m.p.h.	90	42	3	18
"	0.25	"	"	"	90	39	3	31
"	0.25	"	1 sq. ft.	"	91	34	3	42
"	0.125	"	1 sq. yd.	"	90	39	3	50
Purslane								
Aug. 6.....	1.0	60	1 sq. yd.	10 m.p.h.	87	49	4	17
"	0.5	30	"	"	89	47	3	20
Prostrate Pigweed								
Aug. 6.....	0.5	30	1 sq. yd.	10 m.p.h.	90	47	2.3	20
Aug. 12.....	1.0	60	"	12 m.p.h.	89	34	7	17
Knotweed								
Aug. 9.....	0.5	30	1 sq. yd.	12 m.p.h.	90	56	2.3	13
"	0.25	"	"	"	90	59	1.6	25
"	0.125	"	"	"	91	59	2.3	40

INTERCEPTION BY DENSELY AGGREGATED GRASSES

Stink grass (*Eragrostis cilianensis* (All.) Link.), when growing in compact clumps, forms a very effective interception screen by holding water in numerous drops on the leaves, along the stems and in the flowering panicles. Typical clumps of this tufted annual, with flower stalks about 8 inches in height, were arranged to give a natural foliage cover. Interception with an inch of rain in an hour was 18 percent. When one-half inch was applied in 30 minutes, with no air movement, interception was 16 percent. Under similar conditions, except for wind movement of 12 miles per hour, interception rose to 22 percent. Interception increased sharply with decrease in rainfall intensity to 40 percent with one-fourth inch and 62 percent with one-eighth inch in 30 minutes. The dense foliage retained the water for a longer time than for most of the other plants used in these experiments.

Buffalo grass (*Buchloe dactyloides* (Nutt.) Engelm.) is a low-growing native grass rarely attaining a height in excess of 6 inches but forming a dense stand. It has greatly increased its area during the great drought. Sods 18 by 24 inches in area were used in these experiments. The plants dried rapidly after sprinkling but did not show noticeable wilting. With an inch

of rain in 60 minutes, interception was 26 percent. When a half inch was applied in 30 minutes, interception was 17 percent without wind movement and 31 percent under a wind of 12 miles per hour. With rainfall of one-fourth inch, interception increased to 47 percent and with an eighth of an inch 74 percent of the water was held on the plants. These results show strikingly the effect of rainfall intensity and wind movement upon percentage of interception. It helps to explain why a good growth of buffalo grass is so efficient in retarding runoff and how ineffective are light showers in replenishing the moisture supply of the soil (Table 10).

TABLE 10. PERCENTAGE INTERCEPTION BY DENSELY AGGREGATED GRASSES

Date	APPLICATION		Area	Wind	Temp. Deg. F.	Humidity percent	Evap. cc.	Percent
	Inches	Minutes						
Stink Grass								
Aug. 10.	1.0	60	1 sq. yd.	12 m.p.h.	89	42	6	18
"	0.5	30	"	"	89	47	3	22
"	0.5	"	"	None	89	47	0.8	16
"	0.25	"	"	12 m.p.h.	90	47	3	40
"	0.125	"	"	"	90	50	3	62
Buffalo Grass								
Aug. 11.	0.125	30	18x24 in.	12 m.p.h.	90	47	4	74
"	0.25	"	"	"	90	47	3	47
"	0.5	"	"	None	88	49	0.8	17
"	0.5	"	"	12 m.p.h.	87	43	3	31
Aug. 12.	1.0	60	"	"	84	38	7	26

DETERMINATION OF MAXIMUM INTERCEPTION CAPACITY

Sixty-two experiments were performed with 23 different kinds of living or dead plant materials to determine the maximum load of water which they were capable of holding at one time. The interception capacity is expressed in grams of water held. In all experiments the living plants had completed their vegetative growth but were not always in the flowering stage. Materials were chosen from areas of typical height and density of stand. In a few experiments the foliage cover had been reduced slightly by drying of lower leaves or by insect damage.

Big bluestem showed the highest interception capacity of the native prairie grasses. A dense stand, 2 feet in height and without flower stalks, taken from a single square foot, held 217 grams of water. Although the foliage cover of slough grass appeared to be nearly complete, the interception capacity, 77 grams, was much less, due to the small number of stems present and the shedding of leaves from the lower parts of the stems. An area containing psoralea and big bluestem with bluegrass as an understory had an unusually high capacity, 221 grams. An unusually fine growth of buffalo grass, 8 inches in height when in bloom and with many stolons, held 153 grams of water per square foot of area.

Among prairie forbs, tall goldenrod and prairie sage (*Artemisia gnaphalodes* Nutt.) had the highest interception capacity. The goldenrod had about 14 stems per square foot and a height of 64 inches. It held 214 grams. The prairie sage, with 18 stems per square foot and a height of 42 inches, held 261 grams of water.

Among the non-grassy weeds, the saltbush ranked high in ability to intercept rainfall, 182 grams of water being held on the plants which were 2 feet or more in height. The water was held partly as a uniform film and partly as large drops along the margins and at the tips of the leaves.

Stink grass also proved to be very efficient in holding water. Plants averaging 6 inches in height and with many flower stalks held 229 grams. It appears from the results, shown in Table 11, that mat-forming plants do not have as great an interception capacity as plants of upright habit. They not only expose a smaller surface upon which water is held but also their foliage

TABLE 11. MAXIMUM INTERCEPTION CAPACITY OF A SQUARE FOOT OF PLANT MATERIALS IN GRAMS

Living plants	
White sweet clover.....	169
Big bluestem.....	217
Slough grass.....	77
Buffalo grass.....	153
Tall panic grass.....	148
Psoralea, big bluestem, and bluegrass.....	221
Prairie dropseed.....	138
Puncture vine.....	74
Prostrate pigweed.....	47
Spotted spurge ¹	52
Knotweed.....	71
Stink grass.....	229
Tall goldenrod.....	214
Prairie sage.....	261
Bindweed.....	137
Burning bush.....	148
Foxtail ²	137
Saltbush.....	182
Purslane.....	107
Dead plant materials	
Little barley.....	156
Downy brome grass.....	216
Wheat straw mulch.....	445
Russian thistle ³	585

¹*Chamaesyce maculata* (L.) Small.

²*Setaria viridis* (L.) Beauv.

³Single living plant.

is displayed at just one level. Plants with erect stems commonly possess a larger area of foliage and expose it at a number of levels. Water not intercepted by the upper leaves, or water which drips from them, may be held on leaves at any one of several lower levels. Their interception capacity, therefore, is much higher than for plants of prostrate habit. Mat-forming plants are nevertheless effective in protecting soil from erosion (Kramer and Weaver, 1936).

Dead plant materials, while acting as an efficient mulch and protecting the soil from erosion, also prevent a large amount of water from entering the soil. Mats of dead plants of little barley (*Hordeum pusillum* Nutt.) and downy brome grass (*Bromus tectorum* L.), from 1 to 2 inches in thickness, held 156 and 216 grams of water, respectively. An artificial mulch of wheat straw, 4 inches deep, held 19 percent of the rainfall applied at the rate of 1 inch in 30 minutes, or 445 grams.

A single living plant of Russian thistle (*Salsola pestifer* A. Nels.) of rather open form, 20 inches high and 46 inches in diameter, held 585 grams of water. The plant became wetted rather uniformly and many large drops of water also formed in the axils of the spine-like leaves (Fig. 4).



FIG. 4. A single plant of *Salsola pestifer* held 585 grams of water.

INTERCEPTION UNDER NATURAL RAINFALL

Sets of five interceptometers were installed in two prairies and in three fields of planted crops. The amount of water entering the reservoir bottles was measured after each shower or period of rain. Rain gauges were placed in open areas in the immediate vicinity and were read at the same intervals.

Experiments with wheat were begun on May 25, when the plants were about 32 inches high, and were continued until June 22, when the grain was nearly ready for harvest. The field was typical of lowland and had a dense stand. The grain became badly rusted and as a consequence lodged somewhat during heavy rainstorms and windstorms. Maximum interception of 90 percent occurred during a shower of 0.02 of an inch. Interception of 70 percent or more was recorded during several light showers. During a heavy rain followed by showers and mist totaling 1.48 inches one-third of the precipitation was held on the plants (Table 12).

In a field of late oats, the plants averaged 30 inches in height and were fully headed but still green. Interception ranged from 72 percent during a light shower to 45 percent during a heavy rain followed by showers. The oats finally became lodged so badly that further readings were considered valueless (Table 13).

Interceptometers were installed on May 28 in an upland field of alfalfa (*Medicago sativa* L.). The stand was well established and unusually free from weeds. The plants were about 22 inches high and were just coming into bloom. Plants in the experimental area were cut at the same time as those in the adjacent field. Readings of rainfall were taken regularly, but the second growth did not exceed the height of the interceptometers until June 22. From that date until July 7, grasshopper damage became increasingly serious until the plants were so badly stripped of leaves that it was considered useless to continue further. It is not thought that the maximum interception capacity of this crop is indicated. Interception during light

TABLE 12. INTERCEPTION BY A SQUARE METER OF WHEAT IN FIELD UNDER NATURAL RAINFALL

Date of reading	PRECIPITATION		Interception percent
	Inches	Character	
May 27.....	0.24	2 light showers.....	74
June 1.....	0.80	3 showers.....	51
" 6.....	0.07	1 very light shower.....	72
" 10.....	0.06	1 very light shower.....	80
" 11.....	0.02	1 very light shower.....	90
" 14.....	0.35	1 short shower.....	64
" 15.....	0.32	1 short shower.....	52
" 16.....	0.07	1 light shower.....	76
" 21.....	0.46	1 hard shower.....	46
" 22.....	1.48	Heavy rain followed by showers and mist ..	33

TABLE 13. INTERCEPTION BY A SQUARE METER OF OATS IN FIELD UNDER NATURAL RAINFALL

Date of reading	PRECIPITATION		Interception percent
	Inches	Character	
June 25.....	0.15	Several light showers.....	57
" 26.....	0.11	1 light shower.....	72
July 2.....	0.74	Heavy rain followed by light showers.....	45

showers reached a maximum of 89 percent. Interception amounted to 36 percent during two heavy showers registering 0.84 inch. With a heavy rain of 1.8 inches, followed by showers, interception was only 26 percent, but the crop had not reached its normal height and the foliage cover was greatly reduced by grasshoppers (Table 14). On June 22, a rain of 1.45 inches so badly flooded the trench that the reservoir bottles were floated out or buried in mud.

On June 3, interceptometers were installed in a pure stand of slough grass averaging 39 inches in height. Readings were taken without interruption until June 22 when an unusually heavy rain caused complete burial of the interceptometers in silt from adjacent fields. Considering the relatively small number of stems in the quadrat, the foliage cover of slough grass is surprisingly high. This accounts for the effectiveness of this species in intercepting rain even in showers of high intensity. Interception as high as 80 percent occurred during light showers of 0.02 and 0.06 inch. On June 6, with a shower of 0.07 inch, interception was 66 percent while on June 14, with a shower of 0.45 inch, it was 73 percent. This illustrates the importance of the manner in which the rain falls and also the time over which the precipitation occurs (Table 15).

The most complete record of interception was secured in an upland area of big bluestem. On June 3, the plants were about 20 inches in height. The record is complete until August 16,*when the grass had reached its maximum development and was in bloom. The lowest interception was 63 percent obtained on August 15, when the precipitation during a heavy rain and subsequent showers totaled 1.20 inches. Maximum interception of 97 percent was recorded during several very light showers, on August 8, totaling

TABLE 14. INTERCEPTION BY A SQUARE METER OF ALFALFA IN FIELD UNDER NATURAL RAINFALL

Date of reading	PRECIPITATION		Interception percent
	Inches	Character	
June 1.....	0.84	Two heavy showers.....	36
" 6.....	0.12	Light shower.....	70
" 10.....	0.07	Light shower.....	89
" 25.....	0.16	Several very light showers.....	3
" 26.....	0.07	Light shower.....	27
July 2.....	1.80	Heavy rain followed by showers.....	26
" 6.....	0.17	Light showers—pans reset in new area.....	—
" 7.....	0.19	Light showers with wind.....	50

TABLE 15. INTERCEPTION BY A SQUARE METER OF SLOUGH GRASS UNDER NATURAL RAINFALL

Date of reading	PRECIPITATION		Interception percent
	Inches	Character	
July 6.....	0.07	Light shower.....	66
" 10.....	0.07	Light shower.....	76
" 11.....	0.02	Very light shower.....	80
" 14.....	0.45	Hard shower.....	73
" 15.....	0.38	Hard shower.....	78
" 16.....	0.06	Light shower.....	80
" 21.....	0.39	Hard shower.....	67
" 22.....	1.78	Heavy rain followed by showers and mist ..	—

TABLE 16. INTERCEPTION BY A SQUARE METER OF BIG BLUESTEM UNDER NATURAL RAINFALL

Date of reading	PRECIPITATION		Interception percent
	Inches	Character	
June 6.....	0.07	Light shower.....	83
" 10.....	0.07	Light shower.....	86
" 11.....	0.02	Light shower.....	90
" 14.....	0.45	Hard shower.....	70
" 15.....	0.38	Hard shower.....	73
" 16.....	0.06	Light shower.....	80
" 21.....	0.39	Hard shower.....	67
" 22.....	1.78	Heavy rain followed by showers and mist..	68
" 25.....	0.14	Several very light showers.....	79
" 26.....	0.10	Light shower.....	87
July 2.....	1.61	Heavy rain followed by showers.....	68
" 6.....	0.15	Light showers.....	78
" 7.....	0.16	Light shower.....	75
" 19.....	0.58	Rain and showers.....	73
" 22.....	0.10	Several very light showers.....	76
" 26.....	0.12	Very light showers.....	80
" 27.....	0.09	Very light showers.....	89
Aug. 4.....	0.04	Very light showers.....	95
" 8.....	0.06	Very light showers.....	97
" 15.....	1.20	Heavy rain and showers.....	63
" 16.....	0.18	Light shower.....	77

0.06 inch. Interception amounting to three-fourths or more of the total precipitation was common (Table 16). It is quite evident that one reason for the effectiveness of a dense cover of grass in preventing erosion is the large amount of water held on the stems and leaves.

DISCUSSION

It is apparent from the results of these experiments that a large percentage of the rain which falls upon an area covered with vegetation is held on the leaves and stems of the plants. The amount held depends upon a number of factors, among which the kind and density of vegetation are very important. Low-growing or mat-forming plants do not intercept as much rain as plants of greater height because of the smaller surface exposed. A dense cover of prairie vegetation forms a very effective series of screens upon which some of the water may be caught and prevented from reaching the ground. There are at least three such layers in true prairie. The uppermost one consists of the taller grasses and accompanying forbs. The forbs may be of the same or even greater height than the grasses. Below these is a layer of shorter grasses and forbs, while on or near the soil surface there occur many different rosette or mat plants and a few interstitial grasses which complete the vegetative cover. A single stalk of big bluestem with four to seven large leaves presents just that many levels upon which water may be held. The high capacity of prairie vegetation to withhold water is due to the many levels at which interception occurs and the large leaf surface to which water adheres.

Steiger (1930) reported that a square meter of big bluestem from low prairie had a total leaf surface of 6 square meters, including both sides of the leaves. In mixture with other grasses a similar quadrat had a leaf surface of 3 square meters. A pure stand of blue grama grass (*Bouteloua gracilis* (H. B. K.) Lag.) from upland prairie exposed 2.5 square meters of leaf surface. Flory (1936) found that an average square foot of little bluestem and accompanying plants displayed at maturity over 20 square feet of leaf surface as an average for three seasons. The prairie displayed about twice as much leaf surface at maturity, when 15 inches high, as did mature corn when it was 90 inches tall. In connection with the study reported here, similar measurements were made of the leaf surface exposed by typical square-foot areas of big bluestem and slough grass. The measurements included only the fully expanded green leaves and excluded young leaves not completely unfolded, dead leaves, and stems on whose surfaces water also adhered. In the bluestem areas, a few other grasses and forbs were also excluded. The average total leaf surface of a square foot of slough grass was found to be 9 square feet, including both sides of the leaves. The average leaf surface exposed by big bluestem was nearly 12.5 square feet, exclusive of the other species occurring in the area. The extent of the intercepting surface of the prairie grasses and the accompanying forbs is thus seen to be very large.

Horton (1919) concluded that the loss from interception by fully grown field crops may approach for a time that caused by trees. Since the crops are on the ground for only part of the year, the total annual loss would not be so great. If the density of vegetation is not sufficient to cover completely the soil, losses by interception would be much less. Intertilled crops, such as corn and soybeans, form an open canopy of foliage and intercept a smaller percentage of the rainfall than crops, such as alfalfa and clover, whose foliage cover is very extensive.

The amount of water intercepted or, conversely, the amount which reaches the soil and becomes available to the plants depends upon the character of the rainfall as well as upon the kind and density of the vegetation. During light showers or mists all but a very small percentage of the moisture may be held upon the plants, and is evaporated later. This represents a complete loss to the vegetation unless, under especially favorable conditions, some of it may be absorbed, as suggested by Williams (1932). Although the percentage of interception may be high during showers of low intensity, the amount of water held on the plants may not satisfy their storage capacity. During normal rainfall of long duration, a larger percentage of the moisture will reach the ground. Interception is high during light showers and mists or when much evaporation occurs during a rain. In showers of high intensity but of short duration, the storage capacity of the plants is soon reached and the percentage of interception is less than for showers of low intensity.

The percentage of interception loss is also influenced by environmental conditions during the period of precipitation. In nature, it is the aggregate or

collective effects of the factors which are important rather than their individual effects. All of the factors exert their influence upon interception through their effect upon evaporation. Normally the sky is overcast during periods of precipitation, but bright sunshine between showers increases evaporation and, indirectly, interception. Air temperature and relative humidity operating together influence the rate at which the plants dry after being wetted. It is possible for evaporation to occur during a shower since the air is often below the saturation point while rain is falling. Wind movement has a marked influence upon interception through its effect upon evaporation.

Horton (1919) found that many leaves became wetted over their entire upper surface with a film of water which was thicker in the depressions along the veins. More commonly, however, the water accumulated in drops which were concentrated on the elevations between the veins. The drops or blotches of water occasionally overflowed from the edges and wet the under-surface. In the present study, many observations were made, during the progress of the experiments or following showers, concerning the manner in which the water was held on the plants and the ease or difficulty with which the surfaces became wetted. Water was retained principally in the form of a surface film on the prostrate pigweed, on both the cultivated and saw-tooth sunflowers, smartweed, tall goldenrod, willow-leaved aster, field bindweed, saltbush, and Russian thistle. In some of these plants a few drops formed along the margins or at the tips of the leaves and sometimes on the stems. Large amounts of water were held in the flowers of the bindweed, and in the Russian thistle many large drops were formed in the axils of the spine-like leaves.

Water was held principally as drops which often adhered to both surfaces in most of the grasses studied, including the cultivated ones. Drops were commonly formed also on the stems and were especially numerous in the inflorescences. The formation of drops and the amount of water held on big bluestem are shown in Figures 5 and 6. The numerous small drops of water held in a dense sod of buffalo grass are shown in Figure 7. Figure 8 shows the heavy load of water carried by stink grass. Drops were also formed abundantly on purslane, knotweed, kochia, spotted spurge, puncture vine, and prairie sage. In some species the plant surfaces became wetted with some difficulty but after a time drops were formed in the axils of the leaves, at their tips, or along their margins. Examples were spotted spurge, prairie sage, and kochia. There was also a marked difference in the rate at which the plants dried after being wetted. Bindweed, sunflowers, smartweed, tall goldenrod, and buffalo grass dried quickly, while the purslane, stink grass, and prairie grasses retained the water for a longer time. The possible absorption of some water held on the leaves and the effect of the character of the plant surface on interception were not determined.



FIG. 5. Interception of rainfall by *Andropogon furcatus*.

Kiesselbach (1916) reported that for each inch of rainfall 6.5 pounds of water were caught by the leaves and conducted down the outside of a fully grown, well developed cornstalk. This indicates that for this crop some of the water intercepted by the leaves finally reaches the soil and becomes available to the plants. Haynes (1937) found that in soybeans approximately one-third of the precipitation was conducted to the ground by the stems when the plants had reached full vegetative development. In corn, also, the amount reaching the ground in this manner was sufficient to be of significance. In alfalfa, water ran down the stem only after the canopy was thoroughly wetted, while in oats and timothy no measurable amount of water reached the ground by way of the stems.

Observations made during the experiments reported here lead to the conclusion that some water reached the soil by running down the stems but the amount appeared to be small compared with that dripping directly from the leaves. No consistent difference in the results of experiments was obtained when the stems of cut plants were placed in the interceptometer pans or outside. This indicates that in these plants the amount of water running down the stems to the ground is not large. In the light of the studies reported by Williams (1932), it seems improbable that any large amount of intercepted water was absorbed by the plants through their aerial parts.



FIG. 6. The heavy load of water carried by *Andropogon furcatus* is in the form of large drops.

When the amount of water prevented from reaching the soil is expressed in tons per acre, the magnitude of interception by herbaceous vegetation may be more readily appreciated. Based upon their capacity for interception as determined in these experiments, some common plants are capable of holding at one time a total weight of water in tons per acre as follows: bindweed, 6.5; buffalo grass, 7; sweet clover, 8; big bluestem, 10; stink grass, 11; and prairie sage, 12.5. The last two species do not commonly cover large areas but their interception capacity is so great that even small areas are important in withholding water from the soil. When the calculations are based upon the percentage of interception during the application of known amounts of water in given periods of time, the amounts held per acre of vegetation are still larger. When one-half inch of water was applied in 30 minutes, bindweed, for example, in intercepting 13 percent carried a load of 7.5 tons per acre. Other results are as follows: buffalo grass, 31 percent, 17.5 tons; winter wheat, 52 percent, 29 tons; slough grass, 55 percent, 31 tons; and



FIG. 7. Water is held by *Buchloe dactyloides* in the form of numerous small drops.



FIG. 8. *Eragrostis cilianensis* is capable of carrying an exceptionally heavy load of water.

big bluestem, 61 percent, 34 tons. When 1 inch of water was applied in an hour, interception and amounts of water held were: buffalo grass, 26 percent, 29 tons; oats, 43 percent, 48.5 tons; sweet clover, 47 percent, 53 tons; big bluestem with other grasses in upland prairie, 43 percent, 48.5 tons; and pure big bluestem on lowland prairie, 47 percent, 53 tons. When the rainfall was increased to 2 inches per hour, some of the most striking results were: oats, 43 percent, 97 tons; sweet clover, 44 percent, 99 tons; big bluestem, 51 percent, 115 tons; wheat, 58.5 percent, 132 tons; slough grass, 74 percent, 167 tons. The results were unusually high for slough grass because of the density of the stand and conditions favorable to evaporation.

Percentage of interception by different types of vegetation during showers or rainy periods of varying intensity and the amounts of water held are shown in Table 17.

Vegetation plays a variable role in determining how much of the water precipitated will finally enter the soil and become available for absorption by the roots. That a large amount may be intercepted by plants and prevented from reaching the soil, has been shown. Some of the water may be held only temporarily, eventually running down the stems to the ground. This has been shown to be of importance in studies on trees (Horton, 1919) and corn (Kiesselbach, 1916), and may be of some significance among other herbaceous types (Haynes, 1932). Some of the water which penetrates the plant cover may run off instead of being absorbed. Weaver and Noll (1935a) found when 5 inches of water were applied in the form of rain to a prairie plot that runoff was only 3.1 percent. In a stubble field, 27.7 percent of a similar application was lost by runoff, and on fallow ground, where only 4 inches were applied, runoff was 23.3 percent. The same investigators (1935b)

TABLE 17. AMOUNT OF WATER INTERCEPTED BY AN ACRE OF VEGETATION UNDER NATURAL RAINFALL

Date	Vegetation	Rainfall, inches	Interception, percent	Water held, tons per acre
June 22.....	Big bluestem....	1.78	68	136.6
July 2.....	Big bluestem....	1.61	68	123.7
July 19.....	Big bluestem....	0.58	73	47.4
Aug. 15.....	Big bluestem....	1.20	63	85.0
June 1.....	Wheat.....	0.80	51	45.9
June 22.....	Wheat.....	1.48	33	55.1
June 1.....	Alfalfa.....	0.84	36	34.2
July 2.....	Alfalfa.....	1.80	26	52.8
July 2.....	Oats.....	0.74	45	37.6
June 14.....	Slough grass....	0.45	73	37.0

reported runoff, following an application of 2.5 inches of water preceded by 0.91 inch of rain, as follows: prairie, 0; bluegrass sod, 29.3 percent; and bare ground, 50.4 percent. Following the application of 3 inches of water on prairie, 11.3 percent was lost in runoff; from pasture with about two-thirds

bare soil, 50.5 percent; and from a bare area, 71.6 percent. Fredricksen (1938), in comparing the water relations of prairie and alfalfa, found that during the growing season of 1935 average runoff from prairie plots was 1.35 percent while from similar plots of alfalfa it was 14.3, or 10.5 times as great. During the drought season of 1936, runoff from alfalfa exceeded that from prairie 10.8 times.

Native vegetation, especially grassland, is one of the decisive factors in the conservation of water through its effect upon runoff and percolation, as well as checking evaporation by shading the soil. On the other hand, vegetation has an important influence upon losses of water from the soil. That very large amounts are lost through interception, has already been shown. Losses by transpiration from normal prairie averaged almost 32 tons per acre per day over a three-year period (Flory, 1936).

Kittredge (1938) has calculated for different major types of vegetation of the United States the annual water losses due to interception, transpiration, and evaporation. It is noteworthy that in short grass they are as great as those in ponderosa pine, and in tall-grass prairie they are as large as in oak-hickory forest. Additional losses may occur through evaporation where there is no vegetation or by seepage into rock strata but these are small as compared with those brought about by vegetation.

SUMMARY

Interception of rainfall by prairie grasses, weeds, and certain crop plants was measured at Lincoln, Nebraska, during 1937 and 1938.

Pans, 100 cm. long, 4 cm. wide, and 5 cm. deep, were placed beneath the plants with minimum disturbance of the foliage cover. Water applied at predetermined rates to simulate rainfall or natural rain which penetrated the plant cover was measured. The percentage of interception was calculated from this amount.

The percentage of interception varied with the intensity of rainfall, density of foliage cover, and environmental conditions. Wind movement and condition of the sky were especially important because of their effect upon evaporation.

Andropogon furcatus intercepted almost half (47 percent) of an inch of rain during an hour, and larger percentages with applications of lower intensity.

Stipa spartea and *Sporobolus heterolepis* withheld 50 percent or more of the water applied in the form of light showers.

Agropyron smithii intercepted almost half and *Elymus canadensis* more than half of a fourth-inch rain during 30 minutes.

Percentage of interception by *Spartina pectinata* varied from 72 percent with an eighth-inch rain to 55 with a half-inch rain during 30-minute periods.

Lowland forbs withheld from the soil nearly half of the water during heavier showers and about two-thirds during the lighter ones.

Upland forbs intercepted from 20 to over 50 percent of the water falling on them, depending upon the intensity.

Interception by common weeds varied from 34 percent with half-inch rains to nearly 70 percent with eighth-inch showers.

Triticum aestivum prevented nearly 60 percent of the water from reaching the soil during heavy applications of rain and as much as 80 percent with the lowest intensity.

Avena sativa intercepted from 43 to 73 percent of the water applied as showers of varying intensities.

Melilotus alba intercepted the following percentages during an hour: one-eighth inch, 94; one-fourth inch, 92; one-half inch, 57; 1 inch, 47; 2 inches, 44.

Mat-forming weeds held upon their leaves and stems from 9 to 50 percent of the water falling during applications of different intensities.

Eragrostis cilianensis and *Buchloe dactyloides* prevented from reaching the soil amounts of water ranging from 16 percent during heavy rains to 74 percent during light showers.

The maximum capacity of interception ranged from 47 to 261 grams of water per square-foot area of living plant materials. Dead plants held from 156 to 446 grams on similar areas.

Triticum aestivum intercepted 33 percent of heavy natural rainfall and as much as 90 percent of light showers.

Interception by *Avena sativa* varied from 45 to 72 percent of the natural rainfall.

With *Medicago sativa*, interception was as high as 89 percent during a light shower and as low as 26 during a heavy rain.

Interception of natural rainfall by *Spartina pectinata* varied from 66 to 80 percent.

Andropogon furcatus withheld about two-thirds of the precipitation during a heavy rain and as much as 97 percent of very light showers.

Water is held upon plants in the form of thin films or as drops which form on the surface, at the tips, or along the margins of leaves. Water also adheres to the stems.

Extent of the leaf surface and the number of levels at which water may be held are important factors in determining the percentage of interception.

Prairie vegetation has a foliage area 3 to 20 times as great as the soil surface. Leaves are displayed at many levels.

In these experiments, the amount of water reaching the soil by running down the stems was found to be small.

Interception by prairie grasses, weeds, and crop plants results in an important loss of water to the soil. Light showers are ineffective in replenishing the soil water.

Annual losses of water due to interception, transpiration, and evaporation are as high in certain grasslands as in adjacent forested regions.

Interception of rainfall by herbaceous vegetation has an important retarding effect upon runoff and indirectly upon soil erosion.

Grassland is an important factor in the conservation of water through its effect upon runoff and percolation, as well as checking evaporation by shading the soil.

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LIMNOLOGICAL STUDIES IN CONNECTICUT.
PART III. THE PLANKTON OF LINSLEY POND

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LIMNOLOGICAL STUDIES IN CONNECTICUT. PART III. THE PLANKTON OF LINSLEY POND

INTRODUCTION

The results of the first paper of this series suggested the desirability of a more detailed study of the plankton of the Connecticut lakes. In undertaking this work there were three major aims: to compare the various methods of measuring the standing crop of plankton, to attempt an estimate of productivity, and to describe the relationships of the plankton to certain basic environmental factors—light, temperature, and nutrients.

The amount of time required for measurements of the standing crop made it necessary to limit the study to one particular lake. Accordingly, Linsley Pond, which is the most productive of the thermally stratified southern Connecticut lakes, was chosen as the one most likely to yield valuable results. The choice was somewhat unfortunate in that it led to a premature termination of the survey. The work, begun in September, 1937, was forced to an end in June, 1938, when Linsley Pond was treated with copper sulfate to reduce the growth of blue-green algae. The results to be described here are therefore strictly applicable only to autumn, winter, and spring conditions. Any attempt to extend the conclusions to the mid-summer period must remain largely speculative.

I am deeply indebted to my colleagues, who have aided this work in every way possible—to Dr. E. S. Deevey for data on bottom fauna and benthic conditions in general, to Mr. W. T. Edmondson for assistance in the identification of the rotatoria, and to Miss Anne Wollack and Mr. G. E. Hutchinson for material on nutrients and mud analyses. I am particularly grateful to Mr. Hutchinson, whose suggestions and criticisms have been an invaluable help throughout the investigation and during the preparation of the paper.

METHODS

Water samples were collected at Linsley Pond about once a week, and during the entire investigation thirty-six sets of analyses were accumulated. Collections were made at five levels—at the surface and at depths of 2, 5, 9, and 13 meters.

Determinations of the weight of organic matter at the surface and of the chlorophyll at all five levels were made by methods previously described (Riley 1938, 1939). Plankton counts were made at 0, 2, 5, and 9m and occasionally at 13m. Two hundred milliliters of lake water were concentrated to 2.5 ml. by means of a one-second membrane filter. The pore size of the

membranes is $1-2\mu$, so that all except the smallest of the nanoplankton was retained. Counts were made of the animals in 2 ml. of the concentrate and of the phytoplankton in twelve and one-half fields of the Sedgwick-Rafter eyepiece, or 1 ml. of the original lake water. Duplicate counts showed that the difference between the total number of phytoplankton cells in successive counts averaged about 3 percent and was seldom greater than 5 percent. The difference between the counts of a given species was not statistically significant when the total number of cells of the species exceeded 40 per ml. The zooplankton counts were less satisfactory, the average difference between successive counts being 10-15 percent.

The counts served as the basis for rough estimates of the total volume of plankton. Fifty to one hundred members of each species were measured, the results averaged, and the volume estimated by the application of formulae for the volumes of bodies which the species most nearly represented—cylinders, spheres, spheroids, etc.

In order to obtain an estimate of the amount of plankton growth, it was necessary to use the well-known technique of measuring the photosynthesis and respiration of plankton in clear and blackened bottles suspended at different depths. To keep conditions as nearly natural as possible, the bottles were filled with ordinary lake water and were suspended at the same depth from which the sample had been taken. They were generally left in the lake for one week and were then analyzed for oxygen by the Alsterberg modification of the Winkler technique.

Mechanical difficulties prevented the experiments from assuming the proportions of a routine procedure; however, twenty-three sets of surface water data were obtained, and thirteen of the experiments were complete enough to permit the determination of the mean oxygen production and consumption in the entire lake.

THE STANDING CROP

PHYTOPLANKTON COUNTS

The Linsley Pond plankton is composed chiefly of diatoms and blue-green algae, the mean percentages by volume during the period from September, 1937, to June, 1938, being respectively 35 and 25 at the surface and in the entire lake 44 and 28 percent. The amount of blue-greens doubtless would be relatively somewhat higher if it were possible to include the summer period in the average. The green algae constituted about 10 per cent of the volume and were more constant than any other group. The Dinophyceae and Chrysophyceae occasionally formed great blooms, especially in the surface waters. Otherwise they were of little importance.

The most important genera, those which were present in sufficient quantity to appear at least once in the routine counts, are shown in Table 1.

TABLE 1. PHYTOPLANKTON LIST

<i>Myxophyceae</i>	<i>Chlorophyceae</i>
Chroococcus	Staurostrum
Anabaena	Eudorina
Oscillatoria	Ankistrodesmus
Coelosphaerium	Scenedesmus
	Euglena
<i>Bacillareae</i>	<i>Dinophyceae</i>
Fragilaria	Ceratium
Melosira	Peridinium
Cyclotella	
Synedra	
Tabellaria	
Asterionella	
	<i>Chrysophyceae</i>
Mallomonas	Dinobryon

In addition to the genera listed, there were many nanoplankton forms which could not be classified accurately during the course of the plankton counts. For convenience in making volume estimates the cells of these minute forms were placed in arbitrary size groups, one for cells from 2-5 μ in diameter, and the other 5-8 μ . In the final calculation the nanoplankton was all placed with the Chlorophyceae. More careful examination with high power indicated that the quantity actually belonging in other groups was small, probably not more than 10 to 20 percent.

The survey was begun near the peak of the last of the late summer water blooms. It was typical of September blooms in Linsley in that *Fragilaria* was the dominant form, although *Anabaena* and *Coelosphaerium*, the most important organisms of the August blooms, were still present in abundance. By the middle of October the phytoplankton had declined to a normal level, and *Oscillatoria* had become the dominant genus, a position which it maintained throughout most of the winter and early spring. There was no apparent increase in phytoplankton at the time of the autumn overturn, and the chlorophyll maximum which occurred at that time appears to have been a purely physiological phenomenon.

The second great phytoplankton burst, which occurred in January, had a peculiar origin. The water from the larger inlet, being colder than the lake water, spread out in a thin sheet immediately under the ice, covering at least half the lake and perhaps nearly all of it. This water carried large quantities of nutrients and decaying organic matter and was generously seeded with a flora of peridinians, *Cyclotella*, *Mallomonas*, and *Eudorina*, which were presumably derived from the upper of the two lakes. For two weeks these organisms grew rapidly and largely displaced the normal Linsley Pond phytoplankton to lower levels. Subsequently, mixing of the waters took place, with a general decline in the growth rate, and the remnants of the bloom became scattered throughout the lake, where they remained for some time as minor constituents of the plankton.

A mid-winter growth of phytoplankton is apparently not a rare phenomenon in Connecticut lakes. It has been observed in Linsley Pond in other years, and in Quonnapaug. Whether or not the causes were similar on the previous occasions is not known.

The spring phytoplankton burst began shortly after the first of April and persisted until the latter part of the month. It was not marked by the dominance of any one species but was rather a general increase of all the major constituents of the mid-winter period—*Oscillatoria*, *Synedra*, *Melosira*, *Scenedesmus*, peridiniids, and others. During the rest of the spring and until the survey was ended on June 21, these organisms remained in large quantities and in an actively growing condition in the colder water below five meters, while in the surface waters they were largely replaced by a sparser population of *Dinobryon*, *Fragilaria*, and *Asterionella*.

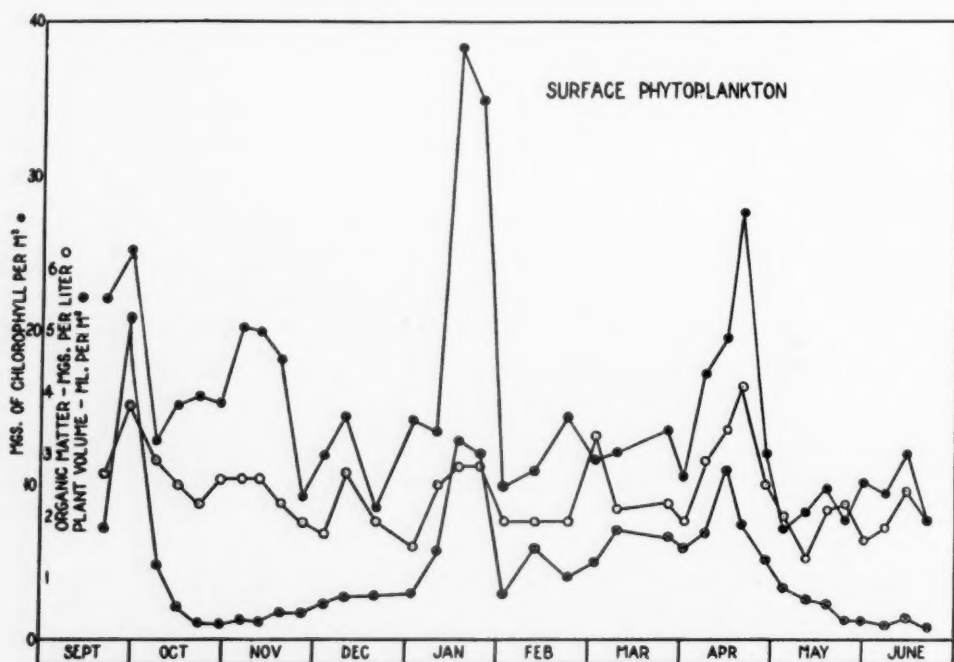


FIGURE 1

The mean number of plant cells in the surface water was 11,200 per ml., and the total range was 2300 to 31,000. The quantity increased with depth to about the five-meter level, where the mean was 14,600 cells per ml.

The seasonal cycle of the estimated total phytoplankton volume, shown in Figures 1 and 2, illustrates the quantitative aspects of the above description. There were maxima in September, January, and April. The January bloom was largely a surface water phenomenon, while the other two were more equally distributed at all depths. In the late spring the mean for the entire lake remained higher than the volume of phytoplankton at the surface

because of the persistence of early spring plankton in the hypolimnion. The total range of plant volumes and the seasonal mean are shown in Table 2.

TABLE 2. PHYTOPLANKTON VOLUMES
(Milliliters per cubic meter)

	Surface	Mean
Maximum	5.208	4.043
Minimum	0.233	0.217
Mean	1.1537	1.1766
Standard deviation	1.0418	0.7084

Because of the great difference in the sizes of the various organisms of the phytoplankton, there was little relation between cell number and volume. In certain cases, as in the mid-winter bloom when the small *Oscillatoria* cells were replaced by large peridinians, there was actually an inverse relation. The coefficient of correlation between volume and cell number in all samples of surface water was .322, which is significant to the five-percent level of probability, but it is much lower than the relationships of volume with chlorophyll and organic matter.

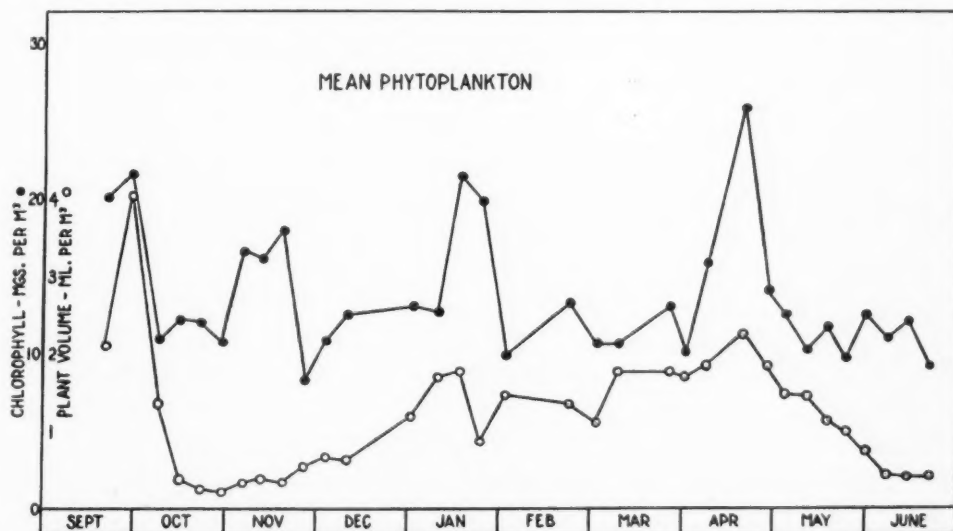


FIGURE 2

CHLOROPHYLL

The quantity of chlorophyll in Linsley Pond and the seasonal cycle are shown in Table 3 and Figures 1 and 2.

TABLE 3. CHLOROPHYLL; MGS. PER M³

Depth in meters	Maximum	Minimum	Mean	Standard deviation
0	38.2	7.1	15.01	7.29
2	31.2	7.6	14.06	
5	24.6	7.8	13.74	
9	24.4	7.1	12.19	
13	23.6	6.3	11.27	
Mean	25.8	8.3	13.58	4.10

The figures show that there is a direct relationship between variations in plant volume and chlorophyll. The three phytoplankton maxima corresponded to the three highest points in the seasonal cycle of chlorophyll, and in only one case, during November, was there a large increase in chlorophyll without a similar increase in phytoplankton volume. The coefficient of correlation is .639 at the surface and .545 in the entire lake. The significance of both these correlations is well below the one per cent level of probability.

There remains, however a considerable residue of non-related variation, too much to be accounted for by technical errors, which are well below ten percent. The relative increase in bloom periods was far from constant, and numerous small unrelated variations occurred.

There is no practical method for dealing with the causes of these variations in an exact way. The data suggest, however, that the causes are both anatomical and physiological.

In the first place, there is some evidence that the quantity of chlorophyll is not constant in all the groups of algae. The ratio of chlorophyll to plant volumes was particularly low during the September bloom and throughout most of the winter and early spring. It was moderately high in the autumn and in the January bloom. The relation of these facts to the qualitative aspects of the seasonal cycle suggests that the quantity of chlorophyll is relatively small in diatoms and blue-green algae and larger in the Chlorophyceae and Dinophyceae. The coefficients of partial correlation of chlorophyll with the various plant groups are as follows: Myxophyceae, .151; Bacillareae, .180; Chlorophyceae, -.404; Dinophyceae, .598; and Chrysophyceae, .574. These figures support the above contention in that the relationship of the first two groups with chlorophyll is significantly lower than that of the last two. The negative correlation between chlorophyll and green algae, however, casts suspicion on the validity of all the figures. It is a result which is theoretically impossible (within the limits of statistical probability) unless it is assumed that there are other factors involved which disturb the normal relationship. In this particular case, the reason seems fairly simple. The quantity of green algae is small and relatively constant. It is never a major constituent during a bloom and frequently decreases at such times, presumably due to failure in the competition for nutrient with the more actively growing dominant species. Since the method of analysis does not take these biological factors into account, it is defective through over-simplification, and the negative correlation is therefore meaningless. This criticism is not readily applicable to the relations of chlorophyll with the other groups of algae, but so simple a treatment of a complex phenomenon is somewhat open to suspicion. Therefore, while there remains a strong probability that the chlorophyll content varies in different forms of algae, more accurate work is required for quantitative description.

The vertical distributions, shown in Figure 3, reveal differences in the chlorophyll-phytoplankton ratio of a physiological nature. The maximum

number of plant cells was found to be somewhere near five meters, while the chlorophyll content was greatest at the surface and decreased fairly regularly to thirteen meters. As will be shown later, its form was intermediate between the curve for oxygen production and the number of plant cells. This suggests chlorosis at the lower depths or a stimulation of chlorophyll production at the surface by the greater light intensity, or perhaps both. Certain aspects of the seasonal cycle also indicate that changes in the chlorophyll-volume ratio, which occurred during short periods of time when the qualitative character of the plankton remained constant, might be dependent on changes in physiological activity. The ratio was generally lower during a bloom than in the intermediate periods, tending to fall the week before the bloom started and to begin to rise again at the time when the phytoplankton reached the highest point or just after it passed the peak.

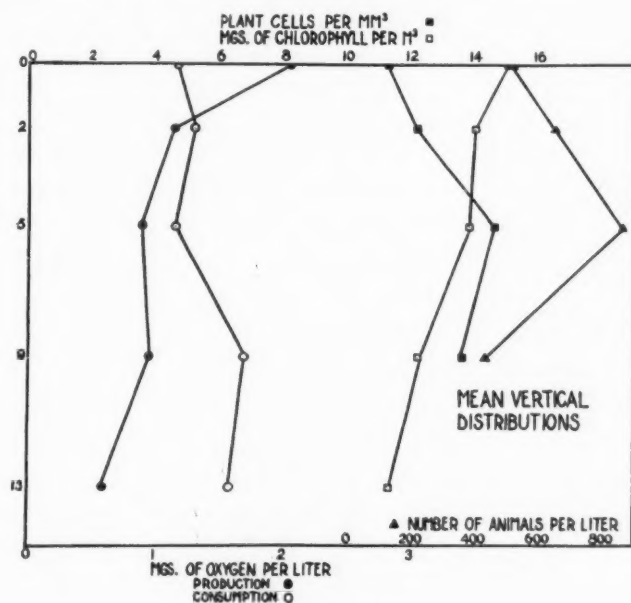


FIGURE 3

ORGANIC MATTER

The dry weight of particulate organic matter in the surface waters of Linsley Pond, obtained by filtration through a 35 second membrane filter of pore size about 0.5μ , averaged 2.37 mgs. per liter, and the total range was 1.3 to 4.1 mgs. The variations in the quantity of organic matter were relatively smaller than those of chlorophyll or phytoplankton volume. The standard deviation of organic matter was approximately one-fourth as large as the mean, while in the case of chlorophyll and volumes the ratios were 1:2 and 1:1 respectively. Otherwise, the seasonal cycles were similar, and the correlations were of the same order of magnitude as the chlorophyll-volume relationship. The coefficient of the chlorophyll-organic matter corre-

lation was .616, and for volume-organic matter it was .609. It is thus evident that the phytoplankton accounts for the major variations in the weight of organic matter and that the total quantity of other constituents—zooplankton, bacteria, and detritus—is relatively constant.

ZOOPLANKTON

The plankton fauna of Linsley Pond is sparse, both in number of species and in total quantity. Among the copepods, only cyclopoids were commonly present; diaptomids appeared in five per cent of the counts, but never in abundance. *Bosmina longirostris* was usually found but never in large numbers, and the only other cladocera were *Chydorus sphaericus* and *Simocephalus exspinosus*. Except for a short period in the middle of the winter, the rotatoria were the most important constituent of the zooplankton. The most common species were the following:

<i>Polyarthra trigla</i>	<i>Collotheca pelagica</i>
<i>P. euryptera</i>	<i>Synchaeta</i> sp.
<i>Ascomorpha</i> sp.	<i>Filinia longiseta</i>
<i>Trichocerca similis</i>	<i>Cephalodella gracilis</i>
<i>T. cylindrica</i>	<i>Conochiloides natans</i>
<i>Pompholyx sulcata</i>	<i>Asplanchna</i> sp.
<i>Keratella cochlearis</i>	<i>Lepidella</i> sp.
<i>K. quadrata</i>	<i>Notholca bostoniensis</i>

Among the protozoa, only *Acanthocystis* appeared regularly. *Anthophysa* and *Epistylis* occurred sporadically, and the latter achieved considerable importance at the time of the January bloom.

The mean number of animals in the Linsley Pond waters and the maximum range are shown in Table 4.

Since the qualitative composition of the zooplankton varied almost as much as that of the plants, it was necessary to calculate the volume of animals in order to obtain an accurate estimate of total quantity. The coefficient of correlation between the number of animals and the volume was .611.

TABLE 4. ZOOPLANKTON; NUMBER PER LITER

Depth	Maximum	Minimum	Mean
0	2940	20	512
2	3560	20	701
5	3530	70	859
9	1260	10	428

The seasonal cycle, shown in Figure 4, bore little resemblance to the phytoplankton curves, and none of the correlations were statistically significant. The estimated mean volume of animals at the surface was 0.2101 ml. per m³, and the total range was 0.009 to 0.913 ml. In the entire lake the mean was 0.2594 ml. and the variation was 0.060 to 1.059 ml. The correlations of phytoplankton with zooplankton volume are shown in Table 5.

The largest quantity of zooplankton occurred in the latter part of November, during the autumn overturn. There was little phytoplankton in the lake at that time but much detritus. Other maxima occurred in early October, a week after the peak of the September phytoplankton bloom, and in January. The latter, composed largely of *Epistylis*, appeared at the same time as the January bloom. Except for this one period, the quantity of animals present during the winter season was very small. It increased during the spring months and remained above the seasonal mean during most of April, May, and June, except in the surface water, where there appeared to be an avoidance reaction.

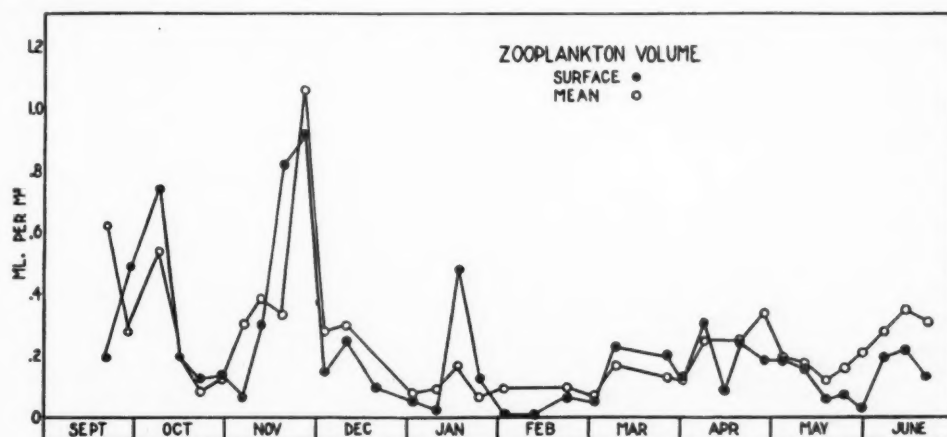


FIGURE 4

TABLE 5. CORRELATIONS OF ZOOPLANKTON WITH PHYTOPLANKTON

	Surface	Entire lake
Chlorophyll-zooplankton207	-.267
Plant volume-zooplankton152	-.234
Organic matter-zooplankton191	—

The mean ratio of phytoplankton to zooplankton volumes was 5.5:1 in the surface water, and the mean for all depths was 4.5:1. The P-Z ratios listed by Ruttner (1937) for several of the east Alpine lakes are all smaller, most of them lying between 1:1 and 1:2. In Linsley Pond there were only two occasions when the ratio was less than 1:1. In Trout Lake (Birge and Juday, 1934) the rotifers and entomostraca constituted about 25 percent of the centrifuge plankton, so that the maximum P-Z ratio was 3:1. In a later section of the paper, it was pointed out on the basis of the analyses of crude protein that the living plants and animals might not constitute more than about 50% of the total centrifuge plankton. Consequently, the P-Z ratio might be as small as 1:1 in Trout Lake. In Lake Mendota, on the other hand, the ratio was about 2:1 in the net plankton, so that if all the phytoplankton were taken into account, the ratio might well be as high as in Linsley Pond. These comparisons indicate, however, that the P-Z relationship is higher in Linsley Pond than in most of the other lakes that have been studied.

OXYGEN PRODUCTION AND CONSUMPTION

The experimentally determined values for oxygen production and consumption are shown in Table 6. Figure 5 is the seasonal cycle of oxygen production at the surface and in the entire lake.

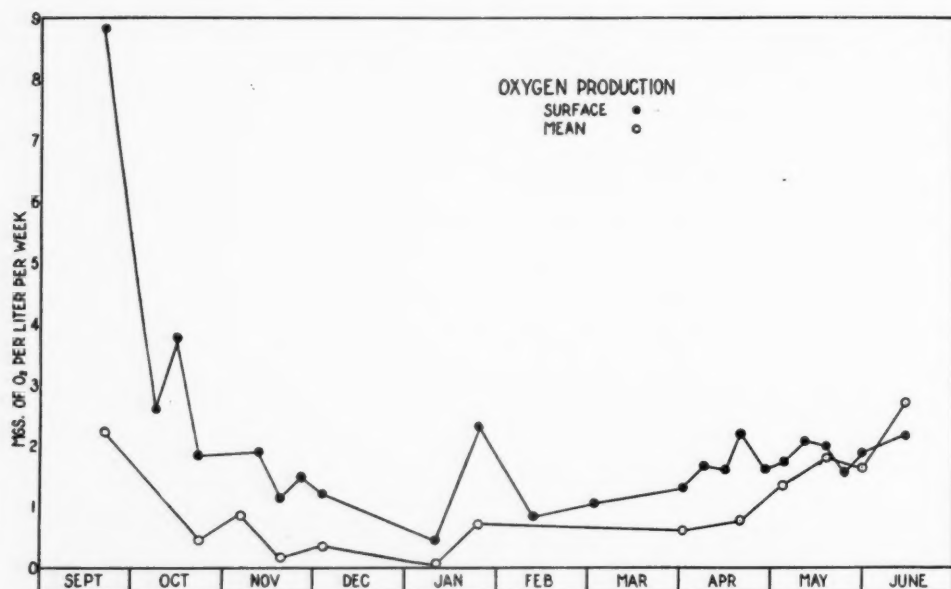


FIGURE 5

TABLE 6. OXYGEN PRODUCTION AND CONSUMPTION; MGS. PER LITER PER WEEK

Depth	Production			Consumption		
	Maximum	Minimum	Mean	Maximum	Minimum	Mean
0	8.83	0.45	2.056	3.30	0	1.156
2	3.48	0	1.133	2.53	0.01	1.297
5	6.12	0	0.898	2.92	0	1.152
9	2.23	0	0.972	6.96	0.21	1.683
13	1.54	0	0.589	3.42	0	1.573
Mean	2.71	0.06	1.065	2.60	0.32	1.359

The experiments were not obtained at equal intervals of time and were especially scanty during the mid-winter period. For this reason the arithmetic mean is not as accurate an estimate of the normal amount of oxygen production and consumption as the average obtained by planimetric measurement of the seasonal curves. The planimetric means were as follows: Oxygen production—surface 1.745, mean 0.821; oxygen consumption—surface 0.956, mean 0.975.

The most marked difference between the seasonal trend of oxygen production and that of the measurements of the standing crop was the winter minimum. The reduction in the activity of the plankton was dependent largely on low temperature, although, as will be shown later, the low light intensity was partly responsible.

The quantity of incident light was determined from tables given by Kimball (1920), which estimate the maximum solar radiation in g. cal. per cm.² for the twenty-first day of each month in the year. The product of the values obtained from the Kimball data and the percentage of the total possible number of hours of sunshine per day, obtained from the New Haven office of the U. S. Weather bureau, was determined for the period of each experiment, and half of the remaining percentage was added as a rough estimate of the radiation from diffuse daylight (Atkins, 1928). The resulting curve, together with the surface and mean temperature of Linsley Pond, are shown in Figure 6.

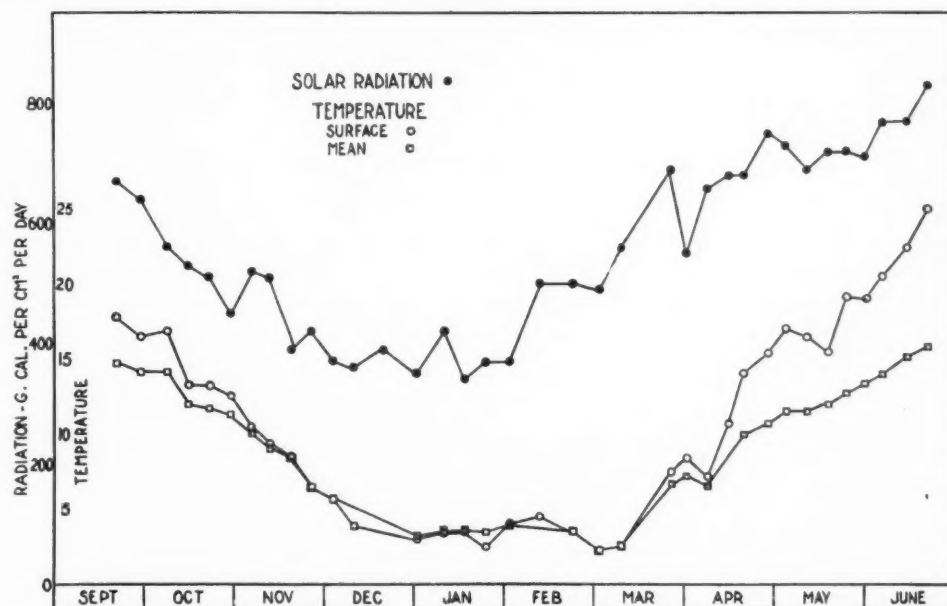


FIGURE 6

In each of the three major blooms, increases in the standing crop were reflected in the quantity of oxygen produced at the surface. After the spring bloom, however, increasing temperature tended to compensate for the decrease in the standing crop, and the oxygen production remained approximately the same.

The mean oxygen production for the entire lake followed the seasonal trend of light and temperature still more closely. The effect of the standing crop was insignificant. The correlations of oxygen production with chlorophyll, temperature, and light are shown in Table 7.

TABLE 7. CORRELATIONS OF OXYGEN PRODUCTION WITH CHLOROPHYLL, TEMPERATURE, AND LIGHT

	Surface	Entire lake
Chlorophyll-oxygen production302	-.089
Temperature-oxygen production360	.810
Light-oxygen production172	.780

The chlorophyll in the surface water was more closely related to the quantity of oxygen produced than the other measurements of the standing crop. The correlation between organic matter and O_2 production was .051, and between volume and O_2 production .150, both of which are statistically insignificant.

It should be noted at this point that because of the fact that there is an abundant and relatively constant supply of bicarbonate and a small amount of free CO_2 , there is no reason to believe that carbon dioxide could have been a limiting factor at any time.

The oxygen consumption was dependent on temperature, the quantity of organic matter, the amount of oxygen available, and to some extent the qualitative composition of the plankton. The relationship between temperature and the quantity of oxygen consumed per mg. of organic matter is shown in Figure 7. The data are fitted with a logarithmic curve, and the correlation

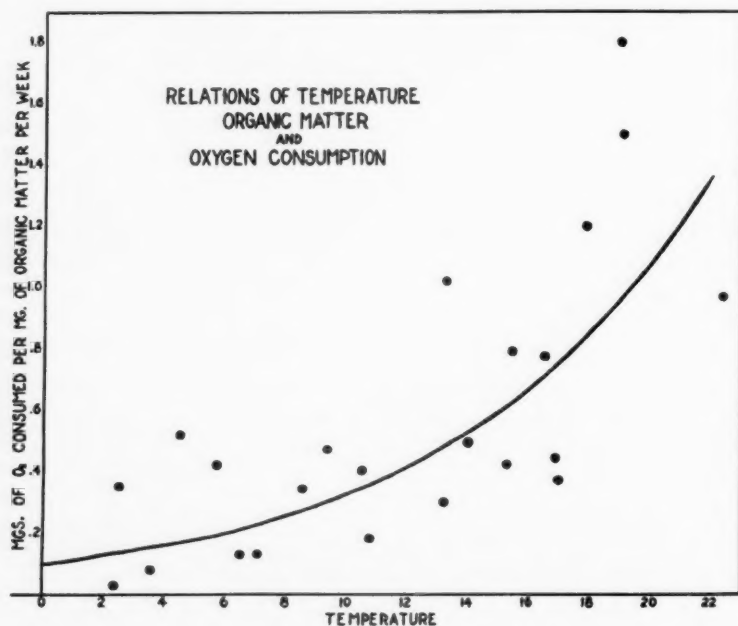


FIGURE 7

is .735. The number of experiments is not sufficient to permit a more complete analysis, but certain other aspects of the problem may be mentioned in passing.

It may be stated *a priori* that the oxygen consumption is not the same for all constituents of the seston. The metabolic rate of the zooplankton is greater than that of the green plants and bacteria, and the latter two may be different. Furthermore, there is a residue of detritus which is a potential rather than an actual consumer. To establish the quantitative aspects of these differences would require a more elaborate set of data, particularly since the relations may not be the same throughout the whole temperature range.

During the middle of November, at the beginning of the autumn overturn, the values for oxygen consumption in the hypolimnion were higher than at any other time in the period of the investigation. They declined to a normal level about the first of December, before the winter stratification was established. It was thus evident that considerable quantities of organic matter and other oxidizable materials had accumulated during the latter part of the summer stagnation period which could not be oxidized because of the low oxygen content and perhaps other unfavorable conditions in the hypolimnion. The autumn overturn removed these barriers and rapid decomposition followed. This phenomenon does not apply directly to the analysis described above, which was concerned only with surface water conditions. It is important to realize, however, that in dealing with the lake as a whole there may be a considerable lag between production and consumption, so that the quantity of organic matter is not in itself an accurate index of either reaction.

Theoretical considerations suggest that there is a systematic error in the experimental technique. Before applying the results to problems of lake productivity, it is therefore necessary to attempt to evaluate the error. This may be done in the following way:

It may be assumed that over an indefinitely long period, the total oxygen production of a lake would equal the oxygen consumption if allowance were made for the increase in consumption caused by the entrance of allochthonous organic matter, and the decrease due to loss of organic matter through the outlet and by permanent sedimentation.

During the period of investigation the mean difference between oxygen production and consumption, as determined by the planimetric method, was -0.154 mg. per liter, or 16 percent.

The loss of seston through the outlet is about 4 percent per week, and it is at least partly compensated by the income of organic matter through the inlets, particularly since the larger of the two inlets is derived from a pond and flows through a swamp, and occasionally has a total organic content (soluble and particulate) of as much as 120 mgs. per liter. This interchange of organic matter may therefore be ignored.

An estimate of the amount of organic matter lost by permanent sedimentation may be made in the following way: Assuming a period of 10,000 years since the retreat of the ice, mud has been deposited in the deepest part of Linsley Pond at a rate of about 1.33 mm. per year (Deevey, 1939). The rate of deposition is less in shallow water, and the average for the entire lake is probably about 0.60 mm. per year, or a total of 57m^3 in the entire lake. The dry weight of organic matter in the unconsolidated surface mud is about 35 mgs. per ml., and at lower depths it is 70-80 mgs. (Hutchinson and Wollack, unpublished). Using 75 mgs. as the most valid figure for the entire column, the rate of deposition of organic matter is about 4.3 metric tons per year. If the carbon content averages half the organic matter, the decrease in potential oxygen consumption is 5.9 metric tons, or 19 percent of the observed

oxygen consumption. The total oxygen consumption (actual and potential) is 36.2 metric tons; the oxygen production, which theoretically should be about the same, is only 25.8 tons. The former is therefore 1.4 times the latter.

In a previous paper (1938a), the author discussed some theoretical considerations which indicate that the observed oxygen production is a minimal estimate, and the observed consumption, a maximal one, of the true values for production and consumption. But in the absence of critical evidence on this subject, or of evidence that the difference between the two estimates is statistically significant (it is not significant if it is permissible to apply standard methods to a somewhat aberrant problem), it seems advisable to regard the true value for oxygen production as lying at some indeterminate point between the two estimates. The mean estimate is therefore 1.2 ± 0.2 times the observed oxygen production.

When corrected in this way, the experiments may be regarded as a fairly accurate measure of the potential photosynthetic activity of the plankton, and events in the bottles would be expected to parallel events in the lake provided the latter are not interfered with by extraneous phenomena, such as turbulence and changes in the quantity of available nutrients. In an investigation now in progress in Long Island Sound it has been found that such a parallelism does exist in marine plankton associations. During periods when the quantity of chlorophyll in the sound is increasing, the oxygen production tends to be higher than when there is a decrease, and the relation between oxygen production and the quantity of chlorophyll in the sea water at the end of the experiment is higher than that between oxygen production and the initial quantity of chlorophyll in the experimental bottles. The relation exists, however, only for three or four days. If the phenomenon exists in Linsley Pond, it does not persist throughout the entire week. The correlation between oxygen production and the quantity of chlorophyll in the lake at the end of the experiment is .155, which is statistically insignificant. It is therefore necessary to qualify the above conclusions by adding that while the experiments represent the potential oxygen production of the plankton, there is no proof that it may not be altered considerably by changing conditions in the lake.

NUTRIENTS

The seasonal cycle of nitrate and phosphate in the surface waters is shown in Figure 8. There was a fairly close relationship between variations in N and P, and the cycles were typical of lakes that are deep enough to be stratified. Winter maxima occurred, and there was a marked reduction of nutrients during the summer stagnation period.

Comparison of the nutrients with the standing crop shows that when the N and P increased, there was generally an increase in the plankton, occurring either at the same time or about a week later. The quantity of nutrients generally began to decrease again just before the phytoplankton reached its

maximum. Since it is reasonable to suppose that the nutrient most effective in controlling the size of the standing crop would be that one which was present in minimum quantities, a compound nutrient curve was estimated as follows: Both N and P were calculated as gram atoms, and the P was multiplied by 20 (conforming to the biological N-P ratio of 20:1 suggested by Cooper, 1937). The lower number of each pair was then chosen as an index of the nutrient most likely to be a limiting factor.

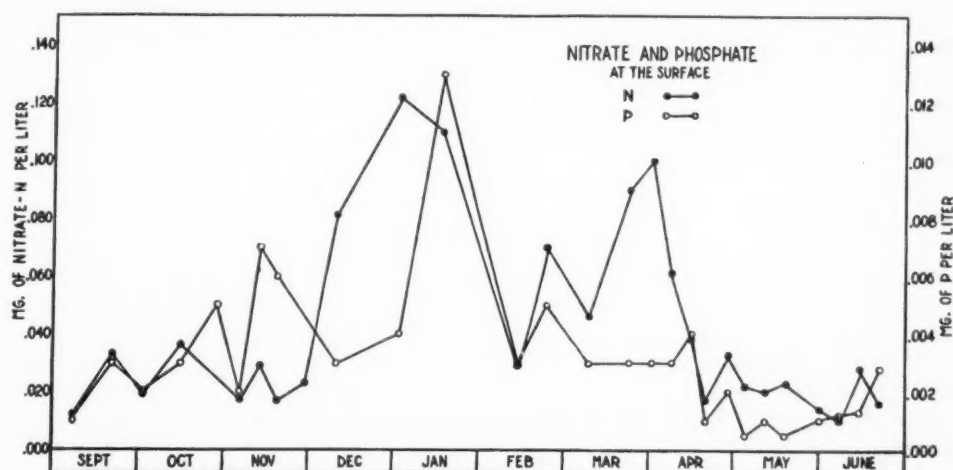


FIGURE 8

TABLE 8. CORRELATIONS OF NUTRIENTS WITH PHYTOPLANKTON

	<i>Chlorophyll</i> (same date)	<i>Chlorophyll</i> (one week later)
N199	.392
P570	.535
N and P553	.578

The correlations shown in Table 8 suggest the following conclusions: Phosphate, having a correlation with chlorophyll that is significant to the 1 percent level of probability, is the more important limiting factor. The immediate effect of nitrate is negligible; the correlation of nitrate with the chlorophyll a week later is slightly significant (5 percent level of probability). The relationship is not improved by the attempt to combine the effects of N and P. The correlations suggest that the lag period for the effect of N is about a week, for P and for the combined effect of N and P it is somewhat less than a week. The curves indicate that the result is an average and that the lag is variable, being longer in the winter and early spring than in the autumn and late spring. There is no evidence of a lag of more than one week. The correlation of N and P with the chlorophyll two weeks later is .151, which is negligible.

The correlations of nitrate and phosphate with oxygen production are all statistically insignificant, and they are not improved by making corrections for independent relationships with temperature and chlorophyll. But although

the correlations show no evidence of a relationship, the situation is too complex to permit a final statement. The oxygen production experiments represent the summation of a series of events over a period of a week. The standing crop of plankton, on the other hand, is merely a momentary balance between the processes of production and consumption. In exactly the same way, the quantity of nutrients represents a temporary balance between regeneration and assimilation. If it were possible to determine the total amount of nutrients used during a given time, in other words a determination more nearly analogous to the oxygen production experiments, the correlation might be higher. At present this must remain a purely theoretical consideration. In the next paper in the present series, by G. E. Hutchinson, the problem of utilization and regeneration of nutrients will be dealt with in more detail.

VERTICAL DISTRIBUTIONS

Certain aspects of the vertical distributions require further description. The curves shown in Figure 3, which are based on the means for the entire period from September to June, are accurate only in so far as they represent the total activities of the plankton at different levels. They are all compounded of different types of curves, so that the averages are somewhat misleading.

During the autumn and winter the curve for oxygen production had a typical exponential form with the maximum at the surface (the true maximum may have been at some unrecorded point between 0 and 2 m.), decreasing sharply from 2.2 mgs. per liter per week at the surface to 0.1 mg. at 5 m. with a further decrease to a negligible quantity at 13 m. During April, May, and June there was a slight decrease in the surface oxygen production and a very marked increase at lower levels. The maximum occurred anywhere between 0 and 9 m. during this period, and the mean was between 1.5 and 2 mgs. at all depths except 13 m., where it decreased to 1 mg. The reasons for the change in the vertical curve were the increased light intensity, which became more effective in the hypolimnion and inhibitory at the surface, the increase in the transparency of the surface waters due to the smaller quantity of plankton, and the large crop of early spring plankton that persisted in the hypolimnion.

There was little seasonal change in the curve for oxygen consumption except for the abnormally high values obtained at 9 and 13 m. during the autumn overturn. These were sufficient to affect the seasonal average; at other times the oxygen consumption was fairly uniform from surface to bottom, but usually slightly greater at 2 or 5 m. than anywhere else.

The point where the curves for oxygen production and consumption cross lies slightly above the 2 m. level. This may be termed the crude compensation point for the entire plankton association. Such evidence as is available indicates that the true compensation point of the phytoplankton varied con-

siderably, from 2 to 9 m. in the autumn and winter and below 9 m. after the middle of April. During May and June the production at 13 m. was always greater than the phytoplankton respiration (according to estimates prepared from the curve in Figure 7 and the estimated weight of phytoplankton as determined in a subsequent section).

During the period from September to April the maximum number of animals and of plant cells was found at 2 m. From April to June the number at 5 and 9 m. increased, and the maximum shifted to 5 m. The number of counts of thirteen-meter water is not sufficient to obtain a seasonal average, but in general, the number of plants and animals was very small during the autumn, until the time of the overturn. From December until June it was only slightly less than at 9 m.

As pointed out above, the mean chlorophyll curve was intermediate between those for cell number and oxygen production. However, the form of the curve was by no means constant. Kozminski (1938), in describing the vertical distribution of chlorophyll in the northeast Wisconsin lakes, listed five common types of distribution. Four of these types were found in Linsley Pond during the course of the investigation. They are as follows:

II. (of the Kozminski classification) Moderately small concentration of chlorophyll at all levels, with less in the hypolimnion than in the epilimnion, and the maximum in the thermocline.

III. Epilimnion moderately poor in chlorophyll, increasing slightly in the thermocline, with a further increase in the hypolimnion and the maximum just above the bottom.

IV. Epilimnion fairly rich, and the chlorophyll decreasing with depth. Maximum at or near the surface.

V. Concentration large at all levels, epilimnion relatively poorest. Large maximum at or under the thermocline and secondary maximum at bottom.

The Kozminski classification is convenient and fairly comprehensive. The different types are undoubtedly significant from the biological point of view. However, the fact that four of the five appeared in Linsley Pond in eight months' time indicates that they have little or no typological value.

ESTIMATED WEIGHT OF PLANKTON IN LINSLEY

On the basis of a preliminary examination, it was reported in the first paper of this series that the phytoplankton of Linsley Pond did not constitute more than 25 percent of the total seston weight. Two methods were used for the analysis—the maximum chlorophyll-organic matter ratio and the regression equation for chlorophyll on organic matter. It was pointed out that both of these methods gave maximal estimates for the weight of phytoplankton.

The estimate obtained from the equation would be accurate if the other constituents, zooplankton, bacteria, and detritus, bore no relation to the quantity of phytoplankton. Since this is not strictly true, the estimate is higher than the true value.

The regression equation for chlorophyll on organic matter, calculated according to the products moments formula is

$$Y = .0519X + 1.59 \quad (1)$$

where Y is the weight of organic matter in milligrams per liter, and X is chlorophyll in milligrams per m^3 . The estimated mean weight of surface phytoplankton according to this equation is 0.78 mg. per liter.

Since data are available for zooplankton, the estimate may be improved by transforming (1) into a multiple regression equation for animals and chlorophyll on organic matter. It is

$$Y = .0405X + .190Z + 1.72 \quad (2)$$

where Z is the volume of zooplankton in ml. per m^3 , and the other symbols are as in (1). The estimated mean weight of phytoplankton is reduced to 0.61 mg. per liter, and the weight of zooplankton is 0.041 mg. While equation (2) is better than (1), it is also a maximal estimate since no allowance is made for errors due to the inter-relation of bacteria and phytoplankton.

The same type of estimate may be made using phytoplankton volumes instead of chlorophyll. The equation is

$$Y = .352X + .268Z + 1.91 \quad (3)$$

where X is the volume of phytoplankton in ml. per m^3 , and the other symbols are as in (2). The estimated mean weight of plants is 0.41 and of animals 0.057 mgs. per liter.

There are two other types of estimates that can be made. The first is based on the maximum chlorophyll-organic matter ratio, which was given in the previous paper as 34:1. The chlorophyll at that time was estimated in Harvey units, and recalculating it in terms of weight of chlorophyll per m^3 to the weight of organic matter in an equal volume of water, the ratio is 30:1000. This ratio is probably slightly too low. Kozminski (1938) listed five values above 30, and the maximum was 38.5. Nevertheless, the ratio of 30:1000 is retained here in order to make the results more readily comparable with those obtained in the preceding paper. The mean weight of phytoplankton according to this ratio is 0.50 mg. per liter. The other type of estimate is based on the volume of plankton. Assuming that the wet weight of the phytoplankton is the same as that of an equal volume of the lake water, the weight of organic matter may be calculated from the volume if the percentage of organic matter is known. The latter cannot be determined very accurately, so that what appears at first to be the best method because of its directness is really one of the most arbitrary. Birge and Juday (1922) suggested that 10 percent was a good average figure, and Ruttner (1937) used the same value. Atkins (1926) and others who worked with marine plankton have assumed that its organic matter was about 25 percent of the ash-free wet weight because the larger seaweeds contain that percentage. Using 10 and 25 percent as extreme limits, the mean weight of phytoplankton in the Linsley surface

water would lie between 0.12 and 0.29 mg. per liter and the zooplankton 0.021 to 0.053 mg. An average estimate of 20 percent would give values of 0.23 mg. per liter for plants and 0.042 for animals.

The fact that all the estimates are of the same order of magnitude indicates that the true value for the weight of plankton lies somewhere near that range. The mean of all the estimates, except that derived from equation (1) which is discarded for reasons stated above, is 0.44 mg. per liter. To regard this mean as the actual weight of phytoplankton, would be arbitrary. It is, however, the best estimate available at present because it not only reduces the basic measurements of the standing crop to absolute terms, but also achieves the best possible balance between their non-related variations, which prevented the adoption of any one of them as an absolute criterion.

Table 9 shows the mean and the total range of the average estimates for the surface water and for the entire lake.

TABLE 9. THE ESTIMATED WEIGHT OF PHYTOPLANKTON; MGS. PER LITER

Surface	<i>Maximum</i>	<i>Minimum</i>	<i>Mean</i>
Phytoplankton	1.17	0.16	0.44
Zooplankton	0.200	0.002	0.047
Residual organic matter	3.3	1.0	1.88
Mean			
Phytoplankton	0.94	0.22	0.40
Zooplankton	0.232	0.013	0.054

According to the various estimates the phytoplankton constituted from 9.7 to 25.8 percent of the seston, with an average of 18.5 percent. The zooplankton was from 1.7 to 2.4 percent, and the mean was 2.0 percent. This gives a mean P-Z ratio of 9.4:1, which is higher than that obtained directly from the volumes.

Of all the measurements of the standing crop, the determination of the volume of animals is most subject to error. Those errors which are not systematic have little effect on the mean volume, but they lower the correlations from which the weight estimates are obtained. The latter are therefore slightly too low. Of the systematic errors in the determination of zooplankton volume, the chief one arises from the necessity of neglecting negative curvatures, e.g. indentations of the ventral surface of the copepod carapace, etc., so that the directly determined volumes are too great. Therefore, the true P-Z ratio probably lies somewhere between the two estimates.

PRODUCTIVITY

DEFINITIONS

When, as frequently happens, the term productivity is loosely used, it is largely because of the technical difficulties involved in its estimation. To use the standing crop as an estimate is attended by obvious inaccuracies. Oxygen deficits and experimental methods are a little better, but they are only rough approximations of the true value. The author believes, however, that these approximations are absolutely necessary to the advance of limnology. If the

results are misleading, they are certainly less so than the more simple estimates, and there is the additional advantage that they pave the way for further elimination of errors. There is no essential difference between such approximations and our measurements of the standing crop. It is obvious from the preceding sections that the latter cannot be measured in any absolute sense without using methods that are prohibitively laborious. It is possible only to make rough estimates which set up maximum and minimum limits, within which the true value lies at some undetermined point. The best estimates of productivity probably will never accomplish any more than this.

The biological productivity of a lake must strictly be defined as the rate of production of organic material in the lake. In the present case, only production in the free water is considered, so that the definition is applied only to plankton production.

In defining phytoplankton productivity it is necessary to make a distinction between the mere synthesis of organic substance, fundamentally glucose, and the elaboration of new organisms from the products of photosynthesis, for although both glucose and protoplasmic material are considered as integral parts of the plant, and are of equal importance in gross determinations of plankton weight, the relatively fixed size of unicellular plants imposes a limit on productivity by mere accretion of stored food, so that synthesis of protoplasm, i.e. reproduction, is the only means of maintaining a permanently productive population.

Since the phytoplankton is part of a food chain which in general shows the phenomenon of the pyramid of numbers, it is desirable, in drawing up definitions of plankton productivity, to expand the concept still further, to include all the categories of the plankton association. These definitions may be stated as follows:

Gross productivity. The rate of production of organic matter by the photosynthetic activity of the phytoplankton.

Phytoplankton productivity. The rate of production of phytoplankton organisms. These either increase or replace the organisms of the standing crop.

Zooplankton productivity. The rate of production of animal plankton.

The zooplankton not being a simple category in the hierarchical food chain, the definition strictly should apply to algal-eating forms, with another definition for the predators. Theoretically, another category in the hierarchy of definitions could be introduced for the macroscopic plankton-feeding nekton. For each definition an efficiency can theoretically be calculated, such an efficiency being the ratio of the rate of production of the type of material in question measured in energy units, to the rate of incidence of solar radiation on the lake surface measured in the same units.

The above definitions are in accord with limnological theory, for they permit the application of standard mathematical procedures to the dynamic aspects of ecological relationships. Technical difficulties, however, prevent

their immediate application to practical limnological problems. The closest approach that can be made at present is an estimate of the mean rate of production during a specified unit of time. But since there appears to be no practical advantage to be gained in dealing with mean rates, the following empirical definitions are proposed:

Gross production. The amount of photosynthetic activity occurring during a given unit of time, expressed as units of glucose, oxygen, energy, or any other term in the equation for photosynthesis.

Phytoplankton production. The quantity of phytoplankton produced during a given unit of time, expressed as the weight of dry organic matter.

The next section is devoted to a discussion of gross production. The problems of phytoplankton production in Linsley Pond are dealt with in another paper (Riley, 1939a), together with an analysis by means of multiple correlations of the relationship of production to environmental factors and a general discussion of the application of correlation techniques to ecological work.

GROSS PRODUCTION

It was shown in a preceding section that the best available measure of the potential photosynthetic activity of the Linsley Pond plankton is a value lying somewhere between the observed values for production and consumption. This value, stated roughly as 1.2 ± 0.2 times the observed oxygen production, may be used, together with the proper conversion factor, to obtain an estimate of gross production in any desired terms. Table 10 shows the gross production of glucose obtained in this way.

TABLE 10. GROSS PRODUCTION OF GLUCOSE; MGS. PER LITER PER WEEK

	Surface	Entire lake
Maximum	9.94 ± 1.66	3.05 ± 0.51
Minimum	0.50 ± 0.08	0.07 ± 0.01
Mean	2.32 ± 0.39	1.20 ± 0.20
Standard deviation	1.78	0.90

Since the errors of the experimental technique appear to be large systematic, it is considered valid not only to present maximum and minimum estimates, but also to analyze the relationship of gross production with environmental factors. The inter-correlations of chlorophyll, temperature, light, animals, and oxygen production at the surface are shown in Table 11. The nutrients are omitted, since the analysis in a preceding section showed that they have no observable effect on photosynthesis.

TABLE 11. CORRELATIONS OF OXYGEN PRODUCTION WITH ENVIRONMENTAL FACTORS

	Chlorophyll	Temperature	Light	Animals
Oxygen production302	.360	.172	.019
Chlorophyll		-.156	-.235	.023
Temperature723	-.089
Light				-.323

Since all the factors are inter-related, it is not possible to determine from the simple correlations exactly how closely a given variable is related to oxygen production. Allowance is made for inter-correlations by calculating the coefficients of partial correlation, which are as follows: oxygen production-chlorophyll, .345; oxygen production-temperature, .475; oxygen production-light, —.080; oxygen production-animals, .025. Only the first two correlations are statistically significant, and therefore the effect of animals and light on oxygen production is regarded as negligible.

In the entire lake, the partial correlations, again obtained by calculation from the simple correlations, are as follows: oxygen production-temperature, .515; oxygen production-light, .380; oxygen production-chlorophyll, .014; oxygen production-animals, —.018. The effects of chlorophyll and animals are statistically insignificant.

The zooplankton might be expected to have a negative effect on oxygen production by feeding on the phytoplankton. But since the correlations are negligibly small, it is evident that the effect, if it occurs at all, is not important.

The light intensity has a direct influence on the mean oxygen production. At the surface, however, it is insignificant when treated as a simple linear regression.

The mean oxygen production appears to be completely independent of the normal variations in the quantity of chlorophyll that occur in Linsley Pond. The simple correlation is —.089 and the partial correlation .014. It is only at the surface that a significant relationship exists. A possible explanation lies in the fact, noted in the first paper of this series, that in Linsley Pond there is an inverse relationship between the transparency and the quantity of seston. It suggests that the favorable effects of an increased standing crop, with an attendant increase in planktogenic detritus, might be counter-balanced by an automatically decreasing light intensity, so that the resultant effect on oxygen production is negligible.

Cursory examinations of other types of environment suggest that the relationship between oxygen production and the standing crop is never very high, and the quantity of phytoplankton probably is not an accurate index of productivity. The correlation obtained in Linsley Pond, however, does not justify any general conclusions in regard to the limits of the relationship. The range of variation is not large enough for a marked effect to be expected, and if, as suggested above, the relationship with transparency is involved, the effect would be greater in Linsley Pond than in most other lakes because of the large standing crop.

In a purely empirical form, however, the result is undoubtedly of importance in a consideration of lake typology, because it suggests that it is possible to have two lakes of identical gross productivity per unit area of surface, in one of which the phytoplankton is kept down to a relatively low level of zooplankton feeding, and in the other of the pair, practically no such

reduction. The first lake would be phytoplankton poor, relatively rich in animals, with a complete metabolism and sediments poor in organic matter; the second would be poor in zooplankton, with large quantities of phytoplankton and a relatively rich organic sediment—in fact, the lakes would be respectively oligotrophic and eutrophic in the manner in which the terms are often used.

OXYGEN DEFICITS

In the first paper of this series it was pointed out that the method developed by Hutchinson (1938) for determining the relative productivity by measuring the hypolimnetic oxygen deficit is not strictly applicable to small, shallow lakes. The ratio of deficit to organic matter was less than in deeper bodies of water, and it was suggested that the cause was photosynthesis in the hypolimnion. The present work deals only with the first two months of the summer stagnation period, but comparison of the deficit with the experiments permits a few additional notes on the subject.

During the period from April 8 to June 21, the total hypolimnetic deficit averaged 141.9 kilos per week (.56 mg. per liter), and the total increase from week to week ranged from —230 to 497 kilos. Since three of the ten analyses gave negative results for the deficit, and moreover, since the average for the seven positive values was only 1.14 mgs. per liter, it is evident that increases were occurring in the hypolimnetic oxygen content as in the previous study.

During the same period there were four experiments that were complete enough to permit the calculation of the total oxygen production and consumption. The mean hypolimnetic oxygen consumption in these experiments was 458 kilos, or 1.81 mgs. per liter. The hypolimnetic oxygen production averaged only 16 kilos less, showing the essential correctness of the earlier conclusion. Further support is gained by the fact that two of the periods when the oxygen content of the lake showed an increase coincided with the two experiments in which the hypolimnetic oxygen production exceeded the consumption.

The lake deficits obtained at the same time the experiments were performed averaged —70 kilos. Thus, the total difference between lake deficit and experimentally determined oxygen consumption was 528 kilos per week, of which 84 percent can be ascribed to photosynthesis and the remainder to turbulence or systematic experimental error.

BIOLOGICAL EFFICIENCY

The mean gross production, determined by the planimetric method, was 0.39 ± 0.15 mgs. of glucose per liter per week. Since the mean depth in Linsley Pond is 6.7 m., this represents a production of 0.62 ± 0.10 mg. per cm^2 per week, or 0.089 ± 0.014 mg. per day. The energy requirement

for the process is $0.334 \pm .056$ g. cal. per cm^2 per day. The total incident radiation was 593.1 g. cal. per cm^2 per day, so that the efficiency of gross production was 0.056 ± 0.009 percent.

These percentages are of course much smaller than the quantum efficiency of the process. Only about half of the total radiation is in the form of visible light, and only part of the latter is used in photosynthesis. Moreover, there are losses due to reflection and absorption. Nevertheless, for comparing the relative efficiency of different lakes, and different types of biocoenoses in general, this method of calculation is probably as useful as any other.

In comparing the biological efficiency of forests and oceans, Krogh (1934) introduced data which are of interest in this connection. According to these figures, in a typical forest with a mass of dry organic matter of 30 kg. per m^2 , the gross production is about 1.5 kg. per m^2 per year. If the total radiation is assumed to be about the same as in the Connecticut region, the efficiency of gross production would be 0.25 percent. Krogh further estimated that in the ocean the quantity of plankton between the surface and 200 meters would average about 30 g. of dry organic matter per m^2 . Although the rate of turnover of plankton is not known, it seems certain that the efficiency of production in the ocean is far less than in the forest, because an equal efficiency would require an annual turnover averaging fifty crops a year in the entire two hundred meter column. To both Krogh and the present author, this seems to be an impossibly high figure. Krogh pointed out that the difference was due to the greater accessibility of nutrients in the terrestrial environment. Another cause would be the absorption of radiation by the water and by detritus and dissolved organic matter. The effect of the latter two factors would of course be much less in the ocean than in lakes.

The estimated efficiency of gross production is about four and one-half times as great in the forest as in Linsley Pond. It is impossible to draw a definite comparison between lakes and the ocean. The efficiency of gross production is less in the shallow waters of the Gulf of Mexico in the Tortugas region than in Linsley Pond, and unpublished work on Long Island Sound suggests that the latter is considerably more efficient than either of the others. But neither of these regions is typical of oceanic areas in general, nor is there any reason to regard Linsley Pond as an average lake. But if Krogh's contention in regard to nutrients is valid, there is good reason to believe that lakes are on the whole more efficient than the ocean; for the regeneration of nutrients is more efficient in the smaller bodies of water.

It is obviously impossible to attempt an estimate of the efficiency of the higher life cycles, since more detailed data are required for both the standing crop of animals and the rate of turnover. In regard to the zooplankton, the efficiency is relatively low, for the lack of a significant relationship between zooplankton and phytoplankton indicates that only a small part of the latter is eaten.

SUMMARY

1. The plankton of Linsley Pond was investigated during the period from September, 1937, to June, 1938. Lists of organisms are given, and the seasonal cycles of chlorophyll, phytoplankton and zooplankton volumes, and the weight of organic matter in the seston are described.

2. Regression equations are used to estimate the weight of plants and animals in the plankton. The agreement of the various calculations is not complete, but they are of the same order of magnitude. According to the mean estimate, the weight of organic matter in the phytoplankton averaged 0.44 mg. per liter at the surface, or 18.5 percent of the total seston weight. The mean weight of animals was 0.047 mg., or 2.0 percent of the total.

3. Oxygen production and consumption experiments were used as the basis for an estimate of the gross production of glucose by the Linsley Pond plankton. The mean estimate for the surface waters was 2.32 ± 0.39 mgs. per liter per week, and in the entire lake it was 1.20 ± 0.21 mgs. The amount could not be estimated more closely than this because of unavoidable errors in the experimental technique. The efficiency of gross production was estimated to be 0.056 ± 0.009 percent.

4. The effects of certain environmental factors on gross production are examined by means of partial correlations. In the surface waters, the size of the standing crop and the temperature are important factors. In the entire lake, light and temperature bear a direct relation to gross production. Variations in the size of the standing crop are of no importance. Nitrate and phosphate appear to have no effect on productivity, although they are closely related to variations in the standing crop.

5. The amount of zooplankton in Linsley Pond is relatively small, about 10 to 20 percent of the quantity of phytoplankton. Variations in the amount of animals do not have a significant effect on gross production or the size of the standing crop of plants.

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